CONTRASTING EFFECTS OF MEAN INTENSITY AND TEMPORAL VARIATION OF DISTURBANCE ON A ROCKY SEASHORE

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Abstract. Understanding the extent to which natural assemblages withstand changes in the regime of disturbance has considerable practical and theoretical interest. In this paper we examine the separate and interactive effects of intensity, temporal variation, and spatial extent of disturbance on temporal variance in assemblages of algae and invertebrates of rocky shores in the northwest Mediterranean. Temporal variation of disturbance is a predictor variable in the experiment, while temporal variance in abundance and number of taxa and in structure of assemblages are response variables. Multivariate analyses detected a positive relationship between intensity of disturbance and temporal variance in the structure of assemblages, while temporal variation of disturbance elicited the opposite effect. Univariate analyses conducted on the most abundant taxa revealed idiosyncratic patterns, while temporal variance in mean number of taxa was greatly reduced by disturbance, with no distinction among levels of intensity, temporal variation, or spatial extent. These outcomes suggest caution in interpreting the results of experiments in which intensity and temporal variation of disturbance cannot be separated. Distinguishing between these traits of disturbance may be key to predicting the ecological consequence of environmental fluctuations, including those expected under modified climate scenarios.

Key words: algal assemblages; Chthamalus stellatus; *climate change effects, predicting; disturbance intensity; Mediterranean, northwest; mid-shore marine invertebrates; patch size; species distribution, abundance, diversity; temporal variation.*

INTRODUCTION

Disturbance plays a critical role in influencing the patterns of distribution, abundance, and diversity of species (Paine and Levin 1981, Sousa 1984, Pickett and White 1985, Petraitis et al. 1989, Shea et al. 2004). Increasing the intensity of disturbance often imposes larger rates of mortality to individual organisms or colonies, but also releases resources that can enhance the local density of populations (Grime 1973, Connell 1978, Huston 1979, 1994, Connell et al. 1997). The response of individual species to disturbance is therefore determined by a tension between increased mortality (or emigration) and new opportunities of colonization (immigration) due to the availability of fresh resources.

Temporal variation in disturbance can affect the outcome of these contrasting forces. For example, the timing of occurrence of disturbance with respect to the periods of reproduction and recruitment of organisms can have drastic effects on the ability of populations to colonize (Dayton et al. 1984, Breitburg 1985, Benedetti-Cecchi 2000*a*). The spatial extent of disturbance is also important in dictating the success of colonization. Disturbed patches that differ in size and degree of isolation from undisturbed areas can be colonized by species with distinct competitive and dispersal capabilities (Keough 1984, Shumway and Bertness 1994). The life-history attributes of individual species are of overwhelming importance in regulating patterns of recruitment and biotic interactions during colonization (Walker and Chapin 1987, McPeek and Peckarsky 1998).

Few studies have examined the effects of intensity, temporal variation, and spatial extent of disturbance simultaneously (but see McCabe and Gotelli 2000). In addition, while many theoretical and empirical studies have investigated the effects of disturbance on diversity (Mackey and Currie 2001, Shea et al. 2004), comparably fewer studies have examined how variable regimes of disturbance affect temporal fluctuations in populations and assemblages (Collins 1992, 2000). This contrasts with the widely reiterated need of understanding the causes of these fluctuations to explain patterns of colonization and extinction of species and to predict trends in functional properties of natural systems such as productivity and stability (Johnson et al. 1996, Micheli et al. 1999, Lundberg et al. 2000, Inchausti and Halley 2003).

A common approach to the study of disturbance is that of manipulating the frequency of events (Collins 2000, McCabe and Gotelli 2000). The manipulation of the frequency of disturbance provides a useful way of investigating the intensity and the temporal patterning of disturbance simultaneously and can be of considerable practical and theoretical interest (Abugov 1982,

Sousa 1984, Huston 1994). In terms of understanding interactions among traits of disturbance, however, frequency has the disadvantage of confounding intensity with temporal variation. Increasing the frequency of disturbance shortens the interval of time between subsequent events, but also exposes assemblages to a larger number of disturbances over the time scale of the study, compared to treatments maintained under low frequency of disturbance. Hence, both overall intensity and temporal patterning of disturbance change with frequency and the relative contribution of each trait remains unknown (Benedetti-Cecchi 2003).

We manipulated levels of intensity, temporal variation, and spatial extent of disturbance in a three-way factorial design and examined the response of mid-shore benthic assemblages of algae and invertebrates to these treatments in the northwest Mediterranean (unless otherwise noted, we will refer to temporal variation of disturbance as the predictor variable in experiments, while temporal variance in abundance and number of taxa and in structure of assemblages will be response variables). These assemblages provide an excellent system to investigate multivariate and univariate patterns of temporal variance over time scales amenable to experimental manipulation, due to their ability to recover quickly after disturbance (Benedetti-Cecchi 2000b).

We predicted that intense disturbances would drive most organisms temporarily extinct in experimental patches, but that quick recovery would reestablish large abundances in short times. Thus, intensity of disturbance would increase temporal variance in response variables, but this effect is expected to decrease with increasing levels of temporal variation of disturbance. Large temporal variation of disturbance implies that events are clustered in time, with periods in which several events occur at short intervals, alternating with periods in which no or few disturbances occur (Benedetti-Cecchi 2003). A series of intense disturbances operating at short intervals is likely to reduce the mean abundance of most organisms for long periods, dampening temporal variance as a consequence of the scaling relationship between the mean and the variance (Taylor 1961). If this is correct, then intensity and temporal variation of disturbance should affect the temporal variance of response variables interactively. Because small patches may undergo faster rates of recovery if organisms in the surrounding habitat can encroach through vegetative growth, as in the case of macroalgae (Sousa 2001), effects of intensity and temporal variation of disturbance were also expected to change in relation to the size of patches.

MATERIALS AND METHODS

The study site

The study was conducted on the exposed rocky shore of Calafuria (43°30′ N, 10°20′ E) in the northwest Mediterranean, between November 2001 and October 2003.

The portion of shore used in the experiment extended from 0 cm to 30 cm above the mean low water level (MLWL). Dominant organisms include the barnacle *Chthamalus stellatus* (Poli), cyanobacteria (*Rivularia* spp.), molluscan grazers (mainly *Patella* spp.) and a variety of encrusting, filamentous, and fleshy algae. Detailed descriptions of these assemblages are reported elsewhere (Benedetti-Cecchi et al. 2003).

The most common sources of disturbance include the mechanical effects of storms and aerial exposure during calm weather and high barometric pressure. Both types of events can remove organisms from the substratum opening patches ranging in size from a few square centimeters up to 1 m². These patches undergo variable patterns of recovery that are spatially variable and strongly influenced by grazing (Benedetti-Cecchi 2000b).

Experimental design

We manipulated levels of intensity, temporal variation, and spatial extent of disturbance in a three-way factorial design and examined the response of mid-shore benthic assemblages of algae and invertebrates to these treatments. A chisel hold on a battery drill was used to generate mechanical disturbances. The experimental design included three undisturbed patches of substratum of 50 × 50 cm as controls and three patches randomly allocated to each combination of the following treatments: (1) large (100 × 50 cm) and small (50 × 50 cm) disturbed patches (these sizes were within the range of sizes of naturally occurring patches; Benedetti-Cecchi 2000b); (2) low (LI), medium (MI), and high (HI) intensity of disturbance, and (3) low (LV), medium (MV), and high (HV) temporal variation of disturbance. The three levels of intensity were generated by repeatedly chiseling the patches one, two, or three times, respectively. The three levels of temporal variation of disturbance were produced by disturbing the experimental patches six times during the course of the study. Treatment LV was obtained by distributing the six events almost regularly in time, so that the variance of the intervals of time between successive disturbances was nearly zero (we refer here to the variance of the predictor variable). Bad weather prevented a perfectly regular distribution of events in time. The other two levels were obtained by distributing the six events more heterogeneously over the course of the study. The 57 experimental patches were distributed along a stretch of shore about 1 km long and marked at each corner with epoxy putty (Subcoat S; Veneziani, Trieste, Italy) for subsequent relocation. A graphical representation of these treatments is illustrated in Appendix A.

The experimental patches always contained some fragments of algae, even when several events of intense disturbance were applied over short periods of time. Thus, the range of intensities we applied experimentally never reached the most severe effects produced

by natural events such as heavy storms, which can breakup the rocks, exposing completely new substratum to colonization.

Sampling and analysis of data

The experimental patches were sampled non-destructively seven times during the study (Appendix A). At each date of sampling the interval of time since the last disturbance necessarily differed among treatments exposed to different levels of temporal variation of this process. To avoid the problem of confounding the two effects, the seven dates of sampling were chosen in such a way that the mean interval of time since the last disturbance was maintained constant across treatments.

Organisms were sampled in three replicate quadrats of 12×8 cm placed haphazardly in each experimental patch at each date of sampling. A plastic frame divided into 24 subquadrats of 2×2 cm was used to obtain visual estimates of cover of sessile organisms; this was done by assigning to each taxon a score ranging from 0 to 4 and adding up the 24 estimates. Final values were expressed as percentages (Dethier et al. 1993). Densities of mobile gastropods were expressed as number of individuals per quadrat. Only the middle portion (50×50 cm) of the large patches was sampled, so that estimates of abundance were obtained at the same spatial scale in large and small patches (McGuinness 1984). Because only small patches were sampled at their borders, edge effects could contribute to the differentiation between small and large patches.

Organisms were identified to the most detailed level of taxonomic resolution that was possible to achieve in the field. Taxa that could not be identified at the level of species or genus were lumped into morphological groups (Littler and Littler 1980, Steneck and Dethier 1994).

Univariate and multivariate analyses were performed to examine the predicted effects of intensity, temporal variation, and spatial extent of disturbance on temporal variance in abundance and number of taxa and in structure of assemblages. Analyses were based on a three-way fixed-model analysis of variance (ANOVA) with intensity, temporal variation, and spatial extent of disturbance as crossed factors. The analyses also included the a priori contrast of ''controls vs. other treatments.'' Dependent variables were measures of temporal variance in abundance of the numerically dominant organisms and of the number of taxa in quadrats (considered as a surrogate measure of diversity) for univariate responses and the multivariate analogues of these measures for multivariate responses. Univariate measures of temporal variance were transformed to the natural logarithm to make variances homogeneous (after Cochran's test). The multivariate measures of temporal heterogeneity were untransformed as variances were homogeneous. SNK tests were used to compare means that differed significantly in ANOVAs. Statistical techniques are described in detail in Appendix B.
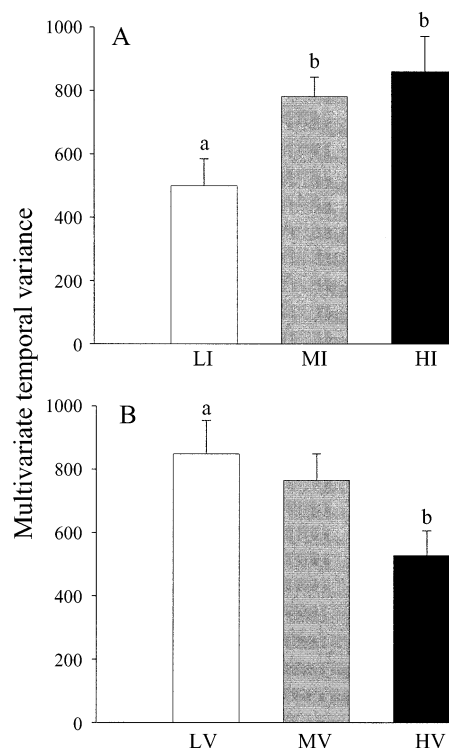

FIG. 1. Multivariate temporal variance illustrating differences among treatments that were significant in the analysis (see Appendix D: Table D1). Data are means + SE. (A) Effect of intensity of disturbance (LI, low intensity; MI, medium intensity; HI, high intensity). Data are pooled across three replicate patches, three levels of temporal variation of disturbance, and two levels of size of patches; $n = 18$ results. (B) Effect of temporal variation of disturbance (LV, low variance; MV, medium variance; HV, high variance). Data are pooled across three replicate patches, three levels of intensity of disturbance, and two levels of size of patches; $n = 18$ results. Bars with the same lowercase letter represent treatments that do not differ significantly at $P < 0.05$ (SNK tests).

RESULTS

Temporal variance in structure of assemblages

A total of 35 taxa were distinguished in this study and used in multivariate analyses. Assemblages in control patches exhibited natural temporal fluctuations that did not differ significantly from those occurring, on average, in manipulated patches (data on temporal changes in control and manipulated patches are reported for several taxa in Appendix C). In contrast, intensity and temporal variation of disturbance significantly affected temporal variance in structure of assemblages (composition and abundance of taxa) (Fig. 1, Table D1 in Appendix D). Mean values of multivariate variance were significantly lower in treatment LI (low intensity of disturbance) than in treatments HI and MI (high and medium intensity of disturbance, respectively) that did not differ significantly (Fig. 1A; SNK test). Significant differences in multivariate variance also resulted in relation to levels of temporal
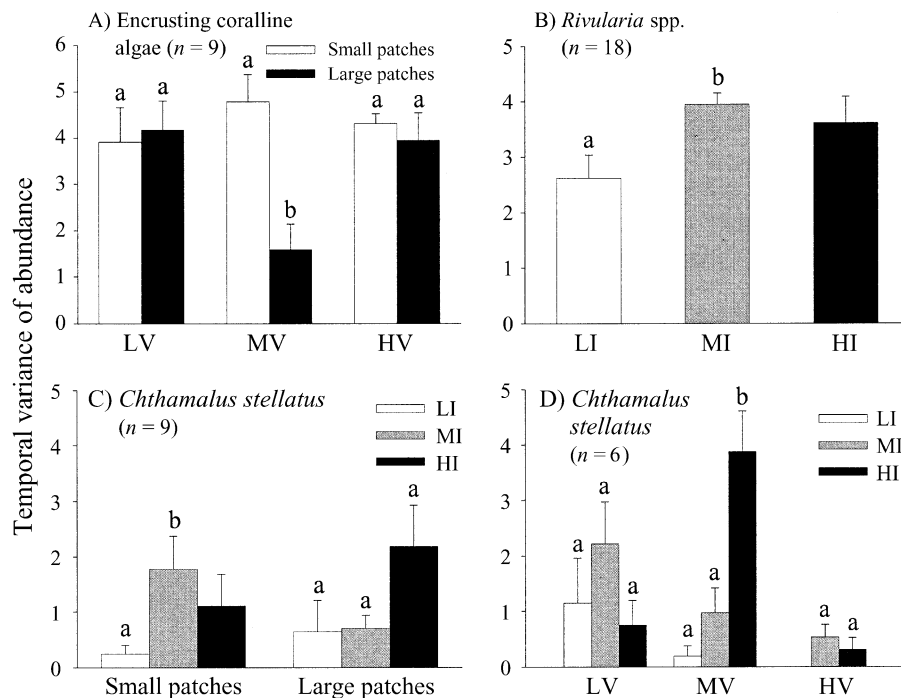
FIG. 2. Univariate measures of temporal variance of abundance (in logarithmic form) for the most abundant taxa, illustrating differences among treatments that were significant in analyses (see Table D2 in Appendix D). Data are means + SE; sample size (*n*) is given in paranthesis. Bars with the same lowercase letter represent treatments that do not differ significantly at *P* < 0.05 (SNK tests). Abbreviations are as in Fig. 1.

variation of disturbance, with lower values under high (HV) than low (LV) variation of disturbance, with the intermediate level (MV) being inconsistently ranked between these two treatments (Fig. 1B; SNK test). The effects of intensity and temporal variation of disturbance disappeared in the analysis based on presence–absence data, which did not detect any significant effect (results not shown).

Temporal variance in abundance and number of taxa

Single taxa exhibited distinct responses to experimental manipulations (Fig. 2). Temporal variance in percentage cover of encrusting coralline algae was significantly larger in small than in large patches, but only in situations of intermediate levels of temporal variation of disturbance (Fig. 2A). Temporal variance in percentage cover of *Rivularia* was significantly larger under medium compared to low intensity of disturbance (MI > LI), with treatment HI being inconsistently ranked between the other two (Fig. 2B). A similar pattern was observed for the barnacle *Chthamalus stellatus* in small, but not in large patches (Fig. 2C). Temporal variance in the percentage cover of *C. stellatus* was also significantly larger in treatment HI compared to treatments MI and LI that did not differ significantly, but only under intermediate levels of temporal variation of disturbance (treatment MV, Fig. 2D). Temporal variance in mean number of taxa did not differ significantly across experimental treatments. Temporal vari-

ance in disturbed patches was, however, 36% less than that of the controls and this resulted in a significant contrast of Control vs. Others. The details of these analyses are illustrated in Table D2 (in Appendix D).

DISCUSSION

This study revealed independent effects of intensity and temporal variation of disturbance on the structure of assemblages. Increasing intensity of disturbance enhanced temporal variance in assemblages, while temporal variation of disturbance elicited the opposite effect. Individual taxa exhibited more complex responses to experimental treatments. Temporal variance in mean number of taxa was greatly reduced by disturbance, with no distinction among levels of intensity, temporal variation, and spatial extent of events.

The simple prediction that high intensity of disturbance would have increased temporal variance in abundance of individual taxa and in structure of assemblages under low, but not under high temporal variation of events, was not supported by the results. We conjectured that a sequence of intense disturbances separated by short intervals of time would have prevented large fluctuations in the biota either by driving most organisms locally extinct, or by reducing their overall abundance to such low levels that large variances would simply not be possible (Taylor 1961). The fact that this did not happen highlights two important features of the system. First, most of the organisms were able to with-

stand even the more extreme combinations of intensity and temporal variation of disturbance, by resisting it and/or by recovering quickly in the disturbed patches. Second, while the percentage cover of barnacles was significantly reduced in disturbed compared to unmanipulated patches, the abundance of encrusting coralline algae and that of limpets increased in the presence of disturbance (though a significant effect was observed only for encrusting algae), as indicated in Appendix C. These results suggest that for some taxa availability of space was more important than mortality and limitation of recruitment in dictating patterns of distribution and abundance. Thus, the response of the assemblage to disturbance was likely to involve both direct and indirect effects, the latter reflecting the reduction in cover of a numerically dominant organism and the subsequent utilization of space by other taxa.

A number of theoretical and empirical studies indicate that environmental fluctuations (related mostly to changes in physical variables) promote the coexistence of species by reducing the intensity of biotic interactions (Hutchinson 1961, Pickett and White 1985, Chesson 1986, Chesson and Huntly 1997). Numerical dominance by one or a few species may be prevented in a system where resources change qualitatively and quantitatively through time, because no single species can incorporate all the life-history attributes necessary to be efficient in every circumstance. Increased temporal variation in abundance of species may also lead to increased risk of local extinction, thereby reducing diversity (Pimm 1991, Lande 1993, Vucetich et al. 2000). Our results, however, do not support this view. The ability of most organisms to colonize quickly after disturbance enabled them to persist throughout the study, despite the fact that virtually all taxa underwent episodic collapses in abundance, which, in some cases, culminated with temporary extinction (Appendix C). Thus, in contrast to the notion that increased variation would imply greater probability of extinction, but in agreement with recent analyses that challenged the generality of this relationship (Inchausti and Halley 2003), our data showed that in a system where organisms recover quickly in disturbed areas, temporal variance of response variables may be positively related to intensity of disturbance not because of compositional changes in assemblages, but because of changes in the relative abundance of taxa. This interpretation is reinforced by the result that effects of intensity and temporal variation of disturbance on assemblages disappeared when analyses were repeated on presence-absence data.

Temporal variation of disturbance may affect assemblages through two main mechanisms. A first mechanism is that high temporal variation of disturbance implies periods of time in which several events occur at short intervals, an extreme condition that may prevent the recovery of even the most fast-growing organisms. A second mechanism focuses on the timing of occurrence of disturbance with respect to the period of reproduction and recruitment of organisms. If the two events coincide and organisms do not release propagules continuously in time (e.g., perennial plants or barnacles), then it is the specific sequence of events rather than temporal variation that can leave strong ecological signatures.

The second mechanism is usually invoked in studies relating temporal variation of disturbance with patterns of recovery (Turner 1983, Breitburg 1985). This might be expected to be the primary mechanism influencing temporal variance in abundance of *Chthamalus stellatus*, because this species recruits mostly in a limited period of time (between May and August on our shores, Benedetti-Cecchi et al. 2000). In principle, a disturbance that coincides with this time should remove most recruits, injecting long-lasting effects on abundance regardless of whether other events occur regularly or heterogeneously in time. Hence, following this reasoning, the intensity × temporal variation interaction documented for this species would reflect an effect of temporal sequence rather than temporal variance of disturbance. This statistical interaction originated as a consequence of a positive effect of intensity of disturbance that occurred only at intermediate levels of temporal variation of events. Does the pattern reflect the absence of disturbance coincidental with the period of recruitment of barnacles for the medium level of temporal variation? The answer is no. By chance, all three levels of temporal variation included at least one event of disturbance between May and August 2002, when recruitment occurred and when the largest fluctuation in abundance of *C. stellatus* was observed (Appendix C). These results cannot be explained simply as a consequence of the timing or sequence of disturbance with respect to the period of recruitment of barnacles. The temporal patterning of events and their cumulative effects over the period of study apparently also played a role. A similar argument applies to the interpretation of the temporal variation × size interaction documented for encrusting coralline algae.

As a note of caution, it is important to say that our experimental design, while suited to tease apart the effects of intensity and temporal variation of disturbance, could not separate the effect of temporal variance (we refer to the variance of a predictor variable here) from the specific sequence of events that we chose to use in order to generate different levels of temporal variation of disturbance. There are many different sequences of events that could still result in levels of variance of the intervals of time between successive disturbances of 2.8, 8.8, and 26.8 as obtained in our experiment for treatments LV, MV, and HV (low, medium, and high temporal vaiance), respectively. To formally investigate this issue would have required the replication of random sequences of events within each level of temporal variation, an approach that was not possible to achieve within the logistical constraints of this particular experiment.

Despite a 100% increase in size between small and large patches (0.5 m^2 vs. 1 m^2), spatial extent of disturbance did not appear to have pervasive effects in the system, in contrast to what has been observed in other studies (Keough 1984, Sousa 1984, Shumway and Bertness 1994). Encrusting coralline algae were the only group of organisms for which larger temporal fluctuations in small patches could be explained as a consequence of quick recovery through vegetative growth (Steneck 1986). Because the size of experimental patches was within the range of sizes of naturally occurring patches (Benedetti-Cecchi 2000*b*), we conclude that spatial extent of disturbance was of minor importance in dictating temporal patterns in this assemblage.

To what extent are our results applicable to other systems? The ability of organisms to recover quickly after disturbance was clearly an important driver of the types of responses observed in the present study. Resilience seems to be a general feature of assemblages of rocky shores. Although disturbance usually results in considerable mortality in these systems, disturbed patches are often limited in spatial extent and intense recruitment associated with vegetative growth from the margins of these patches generally enable fast recovery (Sousa 2001). We suggest that effects of disturbance qualitatively similar to those documented here might be observed in other highly resilient systems. Grasslands, for example, would qualify as resilient systems because grazing and fires usually affect only aboveground biomass, so that belowground vegetation can regenerate quickly (McNaughton 1985, Olff and Ritchie 1998, Cooper et al. 1999). Experiments specifically designed to separate the effects of intensity from those of temporal variation of disturbance are required to test whether or not our conjecture is correct. Regardless of the accuracy of this prediction, our analysis offers insights for interpreting the findings of past experiments on disturbance. This applies in particular to studies that have documented an increase in temporal variance of assemblages with increasing frequency of disturbance (e.g., Collins 2000). The results we have presented here show that intensity of disturbance per se can elicit such a response, whereas increasing temporal variation of disturbance may reduce temporal fluctuations in assemblages.

The ability to separate the effects of intensity and temporal variation of disturbance may provide novel opportunities to investigate how organisms react to fluctuations in their environment. For example, models of climate change predict an increase in the probability of occurrence of extreme meteorological events (Emanuel 1987, O'Brien et al. 1992, Raper 1993, Michener et al. 1997). Models also predict a change in the temporal patterning of these events that would aggregate in short periods separated by prolonged periods of calm weather (Muller and Stone 2001). These changes are likely to affect more the temporal variation than the mean intensity of events over ecological time. Our results would predict a reduction of temporal variance both in the structure of assemblages and in the number of taxa under this scenario.

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APPENDIX A

A diagrammatic illustration of the distribution of events of disturbance over the course of the experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-107-A1.

APPENDIX B

A description of the univariate and multivariate methods of analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E086-107-A2.

APPENDIX C

Data and statistical tests on mean abundance and mean number of taxa in experimental patches are available in ESA's Electronic Data Archive: *Ecological Archives* E086-107-A3.

APPENDIX D

Tables of ANOVA results are available in ESA's Electronic Data Archive: *Ecological Archives* E086-107-A4.