

Connell and Slatyer's models of succession in the biodiversity era

E. MAGGI,¹ I. BERTOCCI,² S. VASELLI,³ AND L. BENEDETTI-CECCHI

Dipartimento di Biologia, University of Pisa, CoNISMa, via Derna 1, Pisa I-56126 Italy

Abstract. Understanding how species interactions drive succession is a key issue in ecology. In this study we show the utility of combining the concepts and methodologies developed within the biodiversity–ecosystem functioning research program with J. H. Connell and R. O. Slatyer's classic framework to understand succession in assemblages where multiple interactions between early and late colonists may include both inhibitory and facilitative effects. We assessed the net effect of multiple species interactions on successional changes by manipulating the richness, composition, and abundance of early colonists in a low-shore assemblage of algae and invertebrates of the northwestern Mediterranean. Results revealed how concomitant changes in species richness and abundance can strongly alter the net effect of inhibitory vs. facilitative interactions on succession. Increasing richness of early colonists inhibited succession, but only under high levels of initial abundance, probably reflecting the formation of a highly intricate matrix that prevented further colonization. In contrast, increasing initial abundance of early colonists tended to facilitate succession under low richness. Thus, changes in abundance of early colonists mediated the effects of richness on succession.

Key words: BEF, biodiversity–ecosystem functioning; colonists; complementarity; density dependence; facilitation; inhibition; low-shore marine assemblage; northwestern Mediterranean; richness; species interactions; succession.

INTRODUCTION

Ecological succession is a key concept with a long history in ecology. It has provided a framework to understand mechanisms of species interaction, coexistence, and dynamics (e.g., Connell and Slatyer 1977, Walker and Chapin 1987, McCook 1994, Pacala and Rees 1998). Starting from the first views of Clements (1916), several models have been proposed to account for temporal patterns of species occurrence and replacement after disturbance (Connell and Slatyer 1977, Huston and Smith 1987, Tilman 1990). The classic facilitation, tolerance, and inhibitory models of succession proposed by Connell and Slatyer (1977; hereafter CS), based on the net effect of early colonists on later ones, have been widely used to classify successional patterns in terrestrial and aquatic systems (Bertness 1991, De Steven 1991, Farrell 1991). In particular, experimental tests of CS models in rocky intertidal systems have been key in unraveling the complexity of successional dynamics within the same assemblage, elucidating some of the mechanisms through which interactions among species and between species and the physical environment may lead to facilitation or

inhibition (Farrell 1991, McCook 1994, Benedetti-Cecchi 2000).

Experimental studies of succession have focused mainly on pairwise interactions between selected species. Focusing on particular species, however, cannot capture the full range of interactions driving succession, particularly in those cases in which recovery is initiated by a diverse assemblage of early colonists, not just by few species. In fact, different early-successional species can have opposite effects on the same later colonist (Turner 1983), or an early organism may enhance or reduce the rate of succession depending on the identity of later species (Bertness 1991). These examples illustrate the potential difficulties inherent in interpreting successional change on the basis of pairwise species interactions, at least in systems where the outcome of these interactions varies greatly with species identity. Determining the net effect of a pool of early colonists on later ones provides an alternative option to unravel the biological mechanisms underlying succession and to predict how differences in the composition of early assemblages affect successional change.

CS models have been examined mainly through manipulation of the presence/absence of interacting species during succession. Although this approach is important in assessing the consequences of species loss on resilience and recovery of assemblages (e.g., Ewanchuk and Bertness 2003), it ignores the consequences of changes in species abundance. This is also an area in need of further research, because changes in species abundance may affect succession through density-

Manuscript received 1 July 2010; revised 31 January 2011; accepted 22 February 2011. Corresponding Editor: J. F. Bruno.

¹ E-mail: emaggi@biologia.unipi.it

² Present address: CIIMAR (Centro Interdisciplinar de Investigação Marinha and Ambiental), Rua dos Bragas 289, Porto 4050-123 Portugal.

³ Present address: Kedrion S.p.A., Loc. Ai Conti, Castelvecchio Pascoli (LU) I-55051 Italy.

dependent processes (Quinn and Dunham 1983, Walker and Chapin 1987) and by influencing competitive and consumer–resource interactions (e.g., Creese and Underwood 1982, Brown and Fridley 2003, Byrnes and Stachowicz 2009).

The framework provided by experimental studies on biodiversity and ecosystem functioning (BEF) offers an opportunity to revisit CS models in terms of net effects of species interactions during succession. In the last 15 years, research on BEF has provided both the concepts and methods to distinguish between complementary and identity effects of species on ecosystem properties and dynamics (e.g., Loreau and Hector 2001, Petchey 2003). These concepts can help to elucidate how changes in the biodiversity of assemblages of early colonists affect subsequent patterns of assemblage recovery. According to the classic formulation of the BEF theory (Hooper et al. 2005), increasing richness of early colonists is expected to increase saturation of available resources through identity or complementary effects, thus slowing down or even preventing successional change (Stachowicz et al. 1999, Van der Putten et al. 2000).

Inhibition through saturation of resources is not the only outcome of succession contemplated by BEF. Facilitation is expected if increasing richness of early-successional assemblages results in the inclusion of facilitative traits, able to positively affect later colonists through provision of limiting resources (i.e., nutrients, space) or by ameliorating stressful environmental conditions (Callaway 1995, Bruno and Bertness 2001), so that the colonization rate of later species is enhanced. BEF can therefore provide a useful framework to assess the net effect of changes in species richness and identity on succession, in scenarios where resource saturation and facilitation may operate simultaneously among different subsets of species (Bulleri et al. 2008).

In this study we tested the general hypothesis that changes in richness, identity, and total abundance of early-successional colonists affected the course of succession in low-shore assemblages of algae and invertebrates in the northwestern Mediterranean, possibly determining shifts between facilitative and inhibitory effects. We used a broad definition of succession, to include any pattern of temporal change in structure (composition and abundance) of assemblages that occurs when new substratum becomes available for colonization. Although succession was originally defined as a directional sequence of species replacements, this concept has been subsequently expanded to include nondirectional changes, such as those that take place when early species are not displaced by later ones (e.g., Platt and Connell 2004). This was also the case in our system, where fast-growing species that initiated succession persisted with slow-growing ones that appeared at later stages (Benedetti-Cecchi and Cinelli 1994, Benedetti-Cecchi 2000) (see Appendix A for further details). We examined how differences in levels of richness, composition, and total abundance of early colonists

influenced subsequent patterns of succession—i.e., the degree of temporal change in the structure of late-successional assemblages and in the abundance of individual taxa within these assemblages. By including abundance as a factor, we tested whether density-dependent processes modulated complementary or identity effects or could explain succession in the absence of these effects. To quantify changes in the structure of assemblages during succession, we used the mean dissimilarity between consecutive times over the duration of the study, calculated separately for each experimental unit. This metric has already been employed to characterize changes in assemblages during succession (e.g., Myster and Pickett 1994, Rebele 2008) and multivariate temporal patterns in general (Collins et al. 2000). These dissimilarity measures enabled us to assess the relative importance of the different mechanisms of succession among treatments. For example, facilitative interactions among species would boost temporal change in assemblages, resulting in larger temporal dissimilarity compared to treatments in which inhibitory mechanisms prevail.

METHODS

Experimental design

The experiment was conducted along the rocky shore of Calafuria, Italy (43°30' N, 10°20' E), between 0 and 0.3 m below the mean low water level (see Plate 1). During July 2004, 140 stainless steel panels of 12 × 8 cm were placed along the rocky shore and screwed to the sandstone substrate. Each panel consisted of 24 sandstone blocks of 2 × 2 × 2 cm each that were individually screwed to the panels to form a uniform surface available for colonization. Panels were left untouched in the field to let early macroalgal species colonize the surfaces. After 11 months, individual blocks were unscrewed and reassembled to synthesize early-successional assemblages using 16 blocks per panel (giving experimental units of 64 cm² in size). We manipulated the most common and abundant morphological algal groups (MG): encrusting coralline algae (mostly *Lithophyllum orbiculatum*), encrusting cyanobacteria (*Rivularia* spp.), green filamentous algae (*Cladophora* spp. and *Chaetomorpha aerea*), red corticated filamentous algae (*Polysiphonia sertularioides*), and red uniseriate filamentous algae (*Ceramium* spp. and *Callithamnion granulatum*). This assemblage consisted of species that are typically found at early stages of colonization on natural substrata in the low-shore habitat (Appendix A; see Benedetti-Cecchi and Cinelli 1994). We assembled experimental panels with one, two, and four MG. One additional treatment with no organisms (zero MG) was added, to mimic patches of open space produced by disturbance events. Encrusting corallines were the only organisms that could monopolize an entire plate during the early colonization stage, so we used only this algal group for the one-MG treatment. In contrast, two randomly synthesized assemblages were initially nested

within richness levels of two and four MG. Two additional assemblages, each with two MG, were included in the experiment to ensure that the taxa characterizing the higher richness level also occurred in the less diversified treatment. This resulted in four and two random assemblages being nested within richness levels of two and four MG, respectively. Each treatment was established at two levels of total abundance (low and high) (see Appendix A for further details on experimental design). These manipulations resulted in a three-way mixed design with richness and abundance as fixed, crossed factors and composition as a random factor nested within richness and crossed with abundance (Benedetti-Cecchi 2004).

To assess the extent to which patterns of colonization on experimental panels resembled those occurring on natural substrata, five additional panels were established at the end of August 2005 and were matched with five clearings produced in surrounding substratum. These new panels and clearings were sampled five times in the following 16 months (see Appendix A for further details).

Sampling and statistical analysis

All panels were sampled six times during the 18-month duration of the experiment (July 2005–December 2006). An interval of about 3 months between sampling dates was appropriate to quantify the rate of change in assemblage structure during succession, based on previous knowledge of recovery rates in this system (Benedetti-Cecchi and Cinelli 1994). The percent cover of organisms was estimated nondestructively (Dethier et al. 1993).

Abundance data of late colonists (i.e., unmanipulated species or morphological groups; see Appendix B for the complete list of species) were analyzed by means of both multivariate and univariate techniques. To quantify temporal change in composition and abundance of assemblages, we calculated the average dissimilarity between all consecutive sampling dates for individual panels using the Bray-Curtis index (Bray and Curtis 1957). This is a semi-metric index that cannot be used directly as a response variable in a linear model (Legendre and Anderson 1999). Hence, before relating multivariate dissimilarity to manipulated factors, we obtained the principal coordinates (Gower 1966) from the Bray-Curtis dissimilarity matrix to place the observations into a Euclidean space, without altering the original distances based on Bray-Curtis index (Anderson 2001). Then, for each panel, the five Euclidean distances between the six consecutive sampling dates were calculated, using the computer program PCO (Anderson 2003), and subsequently were averaged to reflect the mean temporal change experienced by an assemblage on a given panel. These average Euclidean distances were then used as the response variable in a mixed-effect model (Singer and Willett 2003) to examine the effects of richness, composition, and abundance on

average temporal dissimilarity in assemblages. We used the “lmer” function in the program R 2.10.1 for this analysis (R Development Core Team 2010). Richness was a continuous predictor, whereas composition and abundance were categorical predictors; composition was included as a random effect in the analysis. Fixed effects were estimated using maximum likelihood, whereas random effects were estimated using restricted maximum likelihood (Singer and Willett 2003). Linear contrasts based on the Wald statistic (Singer and Willett 2003) were used to examine the overall effect of abundance across levels of richness, in the absence of significant interactions between these factors. The significance of variance components reflecting the effect of assemblage composition was assessed using a likelihood ratio test comparing a full model to a reduced model without the random effect of composition.

We subsequently analyzed temporal variation in percent cover of individual taxa, focusing on the most abundant organisms. These included articulated corallines (mostly *Corallina elongata*), coarsely branched algae, and non-manipulated filamentous algae (these filamentous algae appeared at later stages of succession, mainly as epiphytes of other organisms, even though they were characterized by fast growth rates). Two other species, the brown canopy-forming alga *Cystoseira compressa* and the mussel *Mytilus galloprovincialis*, were included in the univariate analyses even if they did not attain high cover on the experimental plates, because they are important habitat formers at the study site (Maggi et al. 2009). Univariate analyses extended the mixed-effect model used for the multivariate case by including time as a predictor, so that the estimates of linear and quadratic rates of change in abundance of organisms (i.e., the slope of temporal trajectories of abundances) were compared among the different experimental conditions (i.e., at increasing levels of richness and abundance in factorial combinations). Percent cover data (x) were transformed to $\log(x + 1)$ when necessary to improve homoscedasticity (assessed through Q-Q plots and by plotting residuals vs. fitted values). After inspection of raw data, random effects associated with individual experimental units were modeled as a linear and quadratic function of time. Time was centered in all analyses, so that intercepts reflected mean values of response variables at the last sampling date. Effects of assemblage composition were examined using likelihood ratio tests as described in the analysis of Euclidean distances.

RESULTS

Richness (R) and abundance (A) interactively influenced temporal dissimilarity of late-successional assemblages (i.e., the amount of changes in composition and abundance undergone by assemblages through time: $\gamma_{R \times A} = 0.0004 \pm 0.0002$ (all values presented as mean \pm SE unless otherwise indicated), $P < 0.01$). Increasing richness of early colonists reduced temporal change in

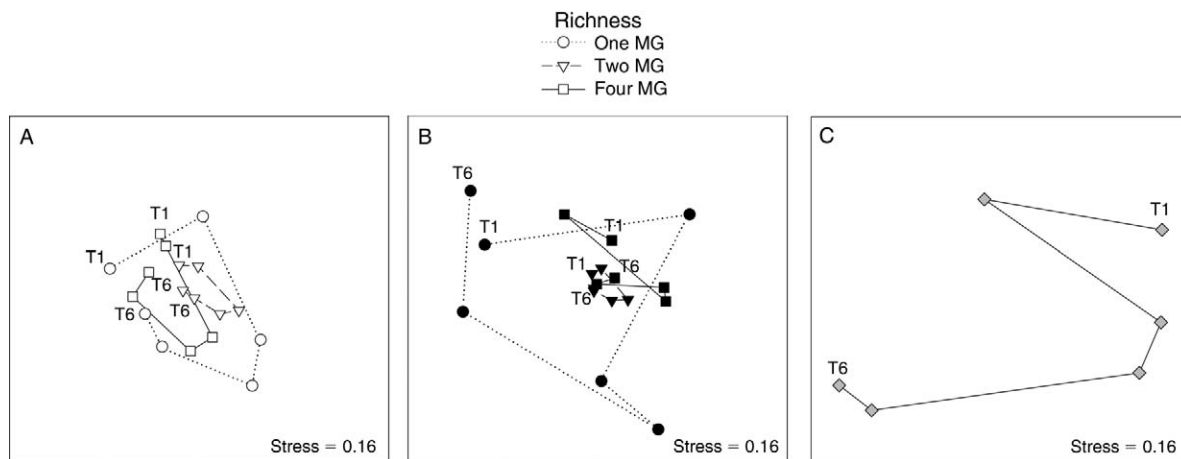


FIG. 1. Nonmetric multidimensional scaling (NMDS) plots showing temporal trajectories from time 1 (T1) to time 6 (T6) of the centroids of late-successional assemblages under different initial levels of richness at (A) low and (B) high abundance or (C) starting as empty panels. A centroid reflects the “average” assemblage at any given point in time. Trajectories are displayed in separate plots (A–C) for clarity but originated from the same NMDS. There were four assemblages contributing to the centroids for the richness level of two morphological algal groups (MG), whereas two assemblages contributed to the centroids for the level of richness of four MG (for details, see Appendix A: Fig. A1). Larger (Euclidean) distances among centroids for a given treatment over time indicate larger temporal changes in structure of assemblages.

assemblages when panels were established at high, but not at low levels of initial abundance ($\gamma_R = -0.0048 \pm 0.0051$, $P > 0.3$). This is indicated by the lower distance among centroids for high compared to low richness levels evident in Fig. 1B (high-abundance treatments), but not in Fig. 1A (low-abundance treatments). In contrast, increasing abundance tended to enhance temporal dissimilarity of late assemblages on panels established with a single taxon ($\gamma_A = -0.0009 \pm 0.0005$, $0.05 < P < 0.06$) (compare the temporal trajectories of centroids for richness level 1 between Fig. 1A and B; see also Appendix C: Table C1). Temporal change in the high-abundance–low-richness treatment combination was as large as that observed on panels that started with zero MG (Fig. 1C). The variance among assemblages (compositional effects for treatments with two and four MG) was not significant (likelihood ratio test: LR = 2.11, df = 1, $P > 0.1$; Appendix C: Table C1).

Most taxa increased in cover during the study period, as indicated by the prevalence of positive linear and quadratic coefficients (Fig. 2; see also Appendix C: Table C2). The effect of richness on linear and quadratic terms was, however, often weakly negative, indicating that the temporal rate of increase in cover was larger in low-richness treatments (Fig. 2). Two notable exceptions were coarsely branched algae and the canopy alga *Cystoseira compressa*. The linear and quadratic terms for coarsely branched algae increased with richness in panels established with high cover of early colonists, whereas the opposite occurred in panels established at low cover (richness \times abundance interactions; linear: $\gamma_{R \times A} = 0.0035 \pm 0.0010$, $P < 0.05$; quadratic: $\gamma_{R \times A} = 0.0002 \pm 0.0001$, $P < 0.05$). The opposite trend, although not significant, was observed for *C. compressa*

(Fig. 2) (linear: $\gamma_{R \times A} = -0.0013 \pm 0.0010$, $P > 0.3$; quadratic: $\gamma_{R \times A} = -0.0001 \pm 0.0001$, $P > 0.2$). Differently, articulated coralline algae showed larger linear ($\gamma_A = 0.0051 \pm 0.0020$, $P < 0.05$) and quadratic terms ($\gamma_A = 0.0003 \pm 0.0001$, $P < 0.05$) under high than low levels of initial abundance with one MG. Linear contrasts indicated that this difference was consistent across all levels of richness (Wald test: for the linear term, $\chi^2 = 4.6$, df = 1, $P < 0.05$; for the quadratic term, $\chi^2 = 7.2$, df = 1, $P < 0.01$). A similar result was observed for *M. galloprovincialis* with one MG ($\gamma_A = 0.0003 \pm 0.0001$, $P < 0.05$) and could not be generalized across richness levels (Wald test: for the linear term, $\chi^2 = 1.1$, df = 1, $P > 0.2$; for the quadratic term, $\chi^2 = 1.8$, df = 1, $P > 0.1$). In contrast, a negative effect of increasing abundance across all levels of richness was evident on final cover of filamentous algae (intercept: $\chi^2 = 4.2$, df = 1, $P < 0.05$) (Fig. 2).

Compositional effects in more diverse assemblages (two and four MG) were not evident (variance components σ^2_{Comp} were not significant for all taxa; likelihood ratio tests, Appendix C: Table C2).

Small individuals of the limpet *P. ulyssiponensis* colonized the experimental panels at densities comparable to those observed in clearings produced in the surrounding substratum (0.68 ± 0.06 limpets per panel [mean \pm SE] and 0.72 ± 0.23 limpets per clearing over the course of the experiment); other herbivores (snails and chitons) were observed occasionally and were not quantified.

The taxa that became established on the additional panels (i.e., those established in August 2005) underwent temporal dynamics similar to those occurring in the scraped patches in the surrounding substratum (Appen-

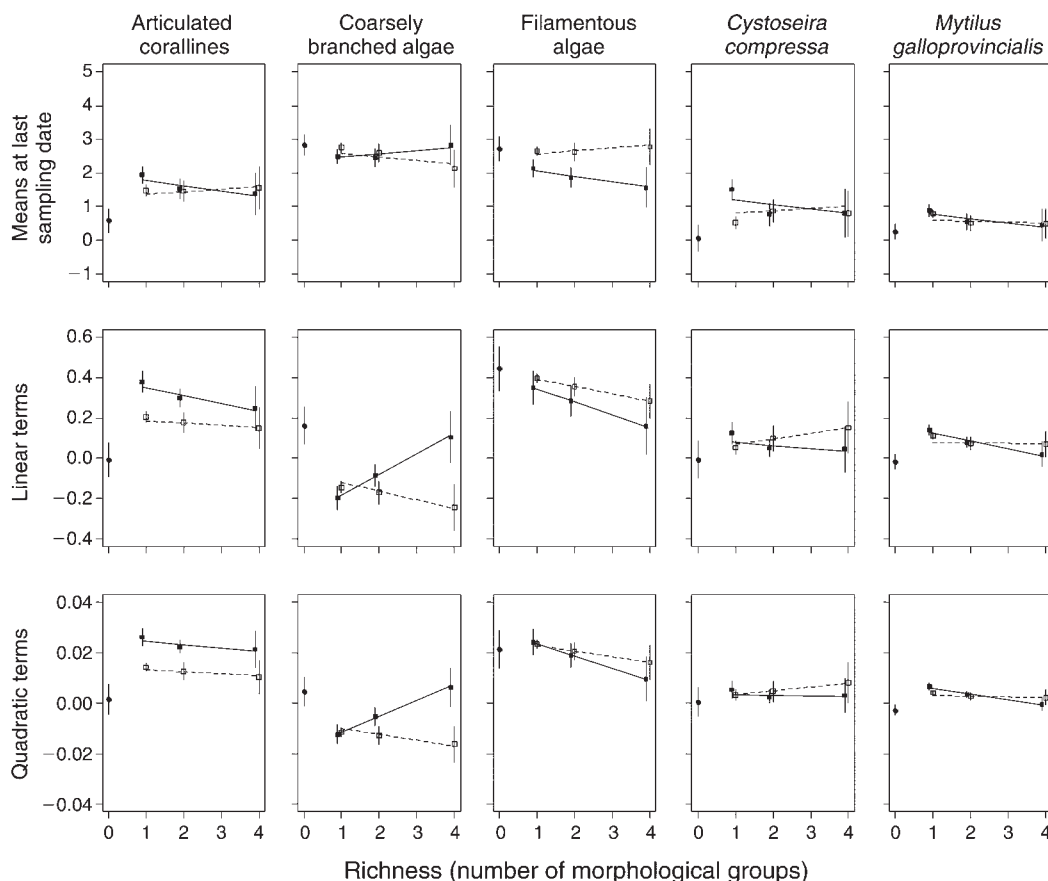


FIG. 2. Effects of richness and abundance on $\ln(x+1)$ -transformed percent cover data of unmanipulated algal taxa. Shown are the fitted means (at the last sampling date) and prototypical trajectories of slopes of temporal trends from regression models, in linear and quadratic terms; error bars are \pm SD. Treatments included experimental units with 0 (solid circles), 1, 2, and 4 morphological groups established at low (open squares and dashed line) and high (solid squares and solid line) abundance. The zero treatment was included in the analysis, but it was not used to fit prototypical trajectories. Positive or negative values of slope in linear and quadratic terms indicate increases or decreases, respectively, in cover of taxa during the study period.

dix A: Fig. A2c), with a shift in dominance between early and late colonists, as observed in the main experiment.

DISCUSSION

According to BEF, increasing richness should lead to increased saturation of available resources through identity or complementary effects (Hooper et al. 2005). As a consequence, we expected a negative effect of richness on the rate of succession, as indicated by other experimental studies in terrestrial and aquatic environments (e.g., Stachowicz et al. 1999, Caldeira et al. 2005, Arenas et al. 2006). Our results indicated that an increase in richness of early colonists inhibited successional change, but only under high levels of initial abundance. There was, in contrast, a trend ($0.05 < P < 0.06$) toward a facilitative effect of increasing abundance of early colonists on temporal dissimilarity of late-successional assemblages for panels that started with one MG (encrusting coralline algae). Hence, changes in

abundance of early colonists mediated the effects of richness on succession.

Stachowicz et al. (1999) highlighted the importance of space monopolization by native assemblages of marine sessile invertebrates in precluding the establishment of nonindigenous species. Increasing richness led to a more efficient use of available space by native assemblages in their study. In our case, in contrast, increasing richness of early algal assemblages was not sufficient to reduce further colonization of the experimental panels and space monopolization per se was not the driving mechanism. Richness hindered succession only in combination with high initial abundances of early colonists, whereas increasing abundance of encrusting corallines alone tended to facilitate succession. These patterns were independent of the availability of open space during the course of the experiment, because space became saturated in about three months in all experimental conditions that started with at least one MG (E. Maggi, I. Bertocci, S. Vaselli, and L. Benedetti-Cecchi, *personal observations*). A possible explanation for our

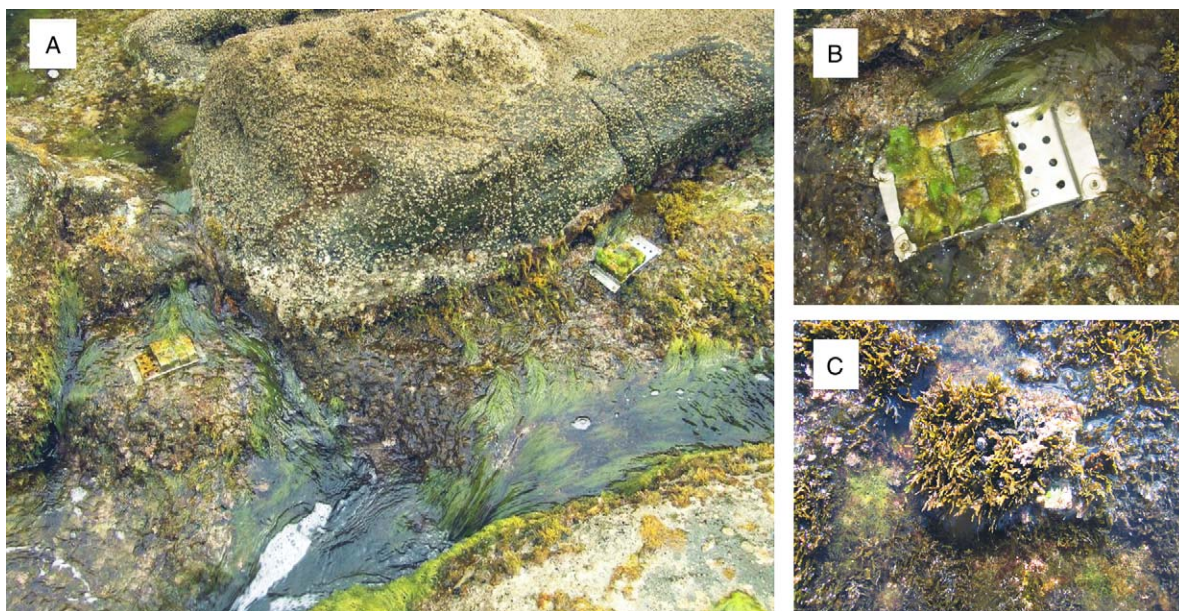


PLATE 1. (A) Experimental panels in a low-shore habitat dominated by turf-forming algae. (B) Encrusting and green filamentous algae on a two-week-old panel. (C) A panel with dense cover of the brown alga *Cystoseira compressa* and some mussels (*Mytilus galloprovincialis*), 18 months after deployment. Photo credits: E. Maggi.

results was that the combination of different morphological algal groups in high-richness treatments formed a highly intricate turf matrix that was less susceptible to further colonization, compared to the relatively simple habitat provided by algal crusts alone or in combination with individual filamentous species (as in two-MG assemblages). It has been shown that turfs can inhibit the recruitment of canopy species in kelp forests (Kennelly 1987) and of *Fucus serratus* in intertidal rock pools (Arenas et al. 2006). In contrast, individual filamentous algae such as *Polysiphonia* and *Ceramium* may have had facilitating effects on settlement of late-successional organisms, as shown for mussel larvae (Bayne 1965). Similarly, encrusting coralline algae may have fostered succession by enhancing settlement and recruitment of later colonists through provision of a structurally simple habitat.

Alternatively, one can speculate that the facilitation trend occurred because of specific attributes of encrusting coralline algae. Several species in this morphological group expose a rough surface with pits and scars that can enhance settlement of algal propagules and invertebrate larvae in comparison to bare rock substrate (Arenas et al. 2006, Bulleri et al. 2009). Similar positive effects of encrusting coralline algae have been reported by a previous investigation conducted in our study area (Airoldi 2000) and were evident in our experiment for mussels and articulated coralline algae.

Identity effects appeared to be unimportant in our analysis, as suggested by the small (and not significant) variance components associated with assemblage terms. Examining differences among random species combina-

tions (assemblages) nested within levels of richness was a major improvement of biodiversity experiments to discriminate between identity and richness effects (e.g., Hooper and Vitousek 1997, Tilman 2001). This approach was suggested as an alternative to including monocultures for all manipulated organisms, which can be logistically unfeasible when there are too many species in play. Including monocultures, however, has the advantage of enabling identity effects to be ascribed precisely to individual species or taxa. Our experimental design included only encrusting coralline algae as “monocultures”; although this design provided a realistic scenario (other taxa were never observed in isolation), the absence of “monocultures” for all manipulated taxa suggests caution in interpreting the lack of identity effects in our results.

The effects that the different levels of richness had on succession, whether positive or negative, became more evident with increasing abundance of early colonists. Density-dependent processes, leading to an increase in interspecific competition, have been identified as a main mechanism responsible for the inhibition of successional change (Walker and Chapin 1987, Stachowicz et al. 1999). Inhibition is the prevalent mode of succession on rocky shores (e.g., Sousa 1979, Underwood et al. 1983, Van Tamelen 1987), although cases of facilitation have been documented in this habitat (Turner 1983, Bertness et al. 1999). Our results suggest that density-dependent effects can underscore both inhibitory and facilitative mechanisms of succession, the former occurring if an increase in abundance of early colonists is also associated with an increase in richness.

A notable exception to this trend was provided by coarsely branched algae, which were facilitated rather than inhibited by the simultaneous increase in richness and cover of early colonists. Although this illustrates once again how variable successional pathways can be, these patterns possibly reflected a positive effect of habitat complexity through the provision of shelter and/or anchoring substrata for settlers of coarsely branched algae, similar to observations of propagules of other algal morphologies (Brawley and Johnson 1991).

Many studies have shown that grazing can have a great impact on succession of algae and invertebrates in rocky intertidal habitats, either hindering or enhancing recovery (Sousa 1979, 1984, Farrell 1991, Benedetti-Cecchi 2000). The small size of limpets and the scarcity of other grazers on experimental panels suggested that grazing was probably of limited importance in our study. Indeed, limpet densities on experimental panels were very similar to those observed in clearings produced in the surrounding habitat, where they did not prevent filamentous algae from attaining high percent cover values.

In spite of intense research on BEF (Naeem et al. 2009), few studies have examined the consequences of biodiversity change for successional dynamics (e.g., Van der Putten et al. 2000). Revealing the community-level effects of inhibitory and facilitative mechanisms can offer important information in the light of present rates of deterioration or loss of natural habitats. Traditional approaches to restoration and conservation focused on negative interactions, through removal of physical or biological threats, and replanting of lost species (Young et al. 2005). Only recently have positive interactions been recognized as playing a fundamental role in conservation planning (Halpern et al. 2007). An integrated approach to the study of successions through BEF methods and concepts has the potential to inform the optimal levels of species richness and abundance that maximize facilitative mechanisms and/or minimize inhibitory ones during recolonization of degraded systems.

ACKNOWLEDGMENTS

We thank M. Incera, M. Mazzi, A. Saettini, and L. Silvestri for assistance in the field, and P. Archambault for helpful comments on a final version of the manuscript. We also thank participants of the BIOFUSE project for stimulating discussions. This is part of a dissertation by E. Maggi at the University of Pisa.

LITERATURE CITED

Airoldi, L. 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. *Ecology* 81:798–814.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.

Anderson, M. J. 2003. PCO: a FORTRAN computer program for principal coordinate analysis. Department of Statistics, University of Auckland, Auckland, New Zealand. (http://www.stat.auckland.ac.nz/~mja/prog/PCO_UserNotes.pdf)

Arenas, F., I. Sánchez, S. J. Hawkins, and S. R. Jenkins. 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. *Ecology* 87:2851–2861.

Bayne, B. L. 1965. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513–523.

Benedetti-Cecchi, L. 2000. Predicting direct and indirect effects during succession in a midlittoral rocky shore assemblage. *Ecological Monographs* 70:45–72.

Benedetti-Cecchi, L. 2004. Increasing accuracy of causal inference in experimental analyses of biodiversity. *Functional Ecology* 18:761–768.

Benedetti-Cecchi, L., and F. Cinelli. 1994. Recovery of patches in an assemblage of geniculate coralline algae: variability at different successional stages. *Marine Ecology Progress Series* 110:9–18.

Bertness, M. D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726.

Brawley, S. H., and L. E. Johnson. 1991. Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. *Journal of Phycology* 27:179–186.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.

Brown, L. R., and J. D. Fridley. 2003. Control of plant species diversity and community invisibility by species immigration: seed richness vs. seed density. *Oikos* 102:15–24.

Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–220 in M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine community ecology*. Sinauer Associates, Sunderland, Massachusetts, USA.

Bulleri, F., J. F. Bruno, and L. Benedetti-Cecchi. 2008. Beyond competition: incorporating positive interactions between species to predict ecosystem invisibility. *PloS Biology* 6(6):e162. [doi:10.1371/journal.pbio.0060162]

Bulleri, F., L. Tamburello, and L. Benedetti-Cecchi. 2009. Loss of consumers alters the effects on resident assemblages on local spread of an introduced macroalga. *Oikos* 118:269–279.

Byrnes, J., and J. J. Stachowicz. 2009. Short and long term consequences of increases in exotic species richness on water filtration by marine invertebrates. *Ecology Letters* 12:830–841.

Caldeira, M. C., A. Hector, M. Loreau, and J. S. Pereira. 2005. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. *Oikos* 110:115–123.

Callaway, R. M. 1995. Positive interactions among plants. *Botanical Review* 61:306–349.

Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Publication 242, Carnegie Institute, Washington, D.C., USA.

Collins, S. L., F. Micheli, and L. Hartt. 2000. A method to determine rates and patterns of variability in ecological communities. *Oikos* 91:285–293.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.

Creese, R. G., and A. J. Underwood. 1982. Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53:337–346.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72:1076–1088.

- Dethier, M. N., E. S. Graham, S. Cohen, and L. M. Tear. 1993. Visual versus random-point percent cover estimations: "objective" is not always better. *Marine Ecology Progress Series* 96:93–100.
- Ewanchuk, P. J., and M. D. Bertness. 2003. Recovery of a northern New England salt marsh plant community from winter icing. *Oecologia* 136:616–626.
- Farrell, T. M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* 61:95–113.
- Gower, J. C. 1966. Some distance properties and latent root and vector method used in multivariate analysis. *Biometrika* 53:325–338.
- Halpern, B. S., B. R. Silliman, J. D. Olden, J. P. Bruno, and M. D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. *Frontiers in Ecology and the Environment* 5:153–160.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Huston, M., and T. Smith. 1987. Plant succession: life history and competition. *American Naturalist* 130:168–198.
- Kennelly, S. J. 1987. Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *Journal of Experimental Marine Biology and Ecology* 112:49–60.
- Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69:1–24.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.
- Maggi, E., I. Bertocci, S. Vaselli, and L. Benedetti-Cecchi. 2009. Effects of changes in number, identity and abundance of habitat-forming species on assemblages of rocky shores. *Marine Ecology Progress Series* 381:39–49.
- McCook, L. J. 1994. Understanding ecological community succession: causal models and theories, a review. *Vegetatio* 110:115–147.
- Myster, R. W., and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 years in 10 contrasting old fields. *Ecology* 75:387–392.
- Naeem, S., D. E. Bunker, A. Hector, M. Loreau, and C. Perrings. 2009. Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective. Oxford University Press, Oxford, UK.
- Pacala, S. W., and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist* 152:729–737.
- Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos* 101:323–330.
- Platt, W. J., and J. H. Connell. 2004. Disturbances and directional replacement of species. *Ecological Monographs* 73:507–522.
- Quinn, J. F., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. *American Naturalist* 122:602–617.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org>)
- Rebele, F. 2008. Vegetation development on deposit soils starting at different seasons. *Plant Ecology* 195:1–12.
- Singer, J. D., and J. B. Willett. 2003. Applied longitudinal data analysis: modeling change and event occurrence. Oxford University Press, New York, New York, USA.
- Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227–254.
- Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatial variable patterns of succession. *Ecology* 65:1918–1935.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3–15.
- Tilman, D. 2001. Distinguishing between the effects of species diversity and species composition. *Oikos* 80:185.
- Turner, T. 1983. Facilitation as a successional mechanism in a rocky intertidal community. *American Naturalist* 121:729–738.
- Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56:202–219.
- Van der Putten, W. H., et al. 2000. Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. *Oecologia* 124:91–99.
- Van Tamelen, P. G. 1987. Early successional mechanisms in the rocky intertidal: the role of direct and indirect interactions. *Journal of Experimental Marine Biology and Ecology* 112:39–48.
- Walker, R., and F. S. Chapin. 1987. Interactions among processes controlling successional change. *Oikos* 50:131–135.
- Young, T. P., D. A. Peterson, and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters* 8:662–673.

APPENDIX A

Description of the experimental design and of successional pathways on experimental panels (*Ecological Archives* E092-118-A1).

APPENDIX B

List of the species included in the multivariate analysis (*Ecological Archives* E092-118-A2).

APPENDIX C

Tables of statistical analyses (*Ecological Archives* E092-118-A3).