RESEARCH ARTICLE

Linking patterns and processes across scales: the application of scale-transition theory to algal dynamics on rocky shores

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Summary

Understanding how species and environments respond to global anthropogenic disturbances is one of the greatest challenges for contemporary ecology. The ability to integrate modeling, correlative and experimental approaches within individual research programs will be key to address large-scale, long-term environmental problems. Scale-transition theory (STT) enables this level of integration, providing a powerful framework to link ecological patterns and processes across spatial and temporal scales. STT predicts the large-scale (e.g. regional) behavior of a system on the basis of nonlinear population models describing local (e.g. patch-scale) dynamics and the interaction between these nonlinearities and spatial variation in population abundance or environmental conditions. Here we use STT to predict the dynamics of turf-forming algae on rocky shores at Capraia Island, in the northwest Mediterranean. We developed a model of algal turf dynamics based on density-dependent growth that included the effects of local interactions with canopy algae. The model was parameterized with field data and used to scale up the dynamics of algal turfs from the plot scale (20×20 cm) to the island scale (tens of km). The interaction between nonlinear growth and spatial variance in cover of turfing algae emerged as a key term to translate the local dynamics up to the island scale. The model successfully predicted short-term and long-term mean values of turf cover estimated independently from a separate experiment. These results illustrate how STT can be used to identify the relevant mechanisms that drive large-scale changes in ecological communities. We argue that STT can contribute significantly to the connection between biomechanics and ecology, a synthesis that is at the core of the emerging field of ecomechanics.

Key words: algal dynamics, ecological experiments, environmental heterogeneity, nonlinear averaging, scale transition, spatial variance, temporal dynamics.

Introduction

Concerns about the ecological and societal consequences of the continuing loss of biodiversity have motivated the analysis of diversity patterns at regional and global scales, in relation to potentially important environmental drivers (e.g. air and sea-surface temperature, CO_2 and nutrient concentrations) (Lotze et al., 2006; Worm et al., 2006; Halpern et al., 2008). Through a correlative approach it is possible to identify putative causal links between predictor and response ecological variables, but correlation does not necessarily imply causation, which is the level of inference that pertains to experiments. Nonetheless, experiments play little role in this (macro)ecological research program (Brown, 1995), despite their enormous contribution to our understanding of the processes that regulate local patterns of species distribution, abundance and diversity and the consequences that changes in these patterns have for the functioning (e.g. productivity and stability) of ecological systems (e.g. Loreau et al., 2002).

A main criticism directed to manipulative field experiments is that they are limited in scope, often as a consequence of logistic constraints: the small size of experimental units (the usual plot size is in the range of hundreds of square centimeters to a few square meters) and the limited spatial and temporal extent over which these units are distributed (usually from tens to hundreds of meters in space and from months to a few years in time) raise concerns on the possibility of extrapolating experimental outcomes over broad scales in space and time (Lawton, 1999; Maurer, 1999). Experimental ecologists have responded to this criticism in different ways: by manipulating whole ecosystems such as lakes (Carpenter et al., 1995; Pace et al., 2004), through the replication of experiments at multiple sites and over time to effectively increase the spatial and temporal extent of the investigation (e.g. Benedetti-Cecchi et al., 2000) and by embedding local manipulative studies into regional correlative analyses (Hewitt et al., 2007).

Modeling offers another approach to address large-scale ecological problems. Interesting recent developments include reaction–diffusion, integro-differential and coupled-map lattice models to scale up organismal dispersal and movement from local scales to entire ecosystems (Hastings et al., 2011). Modeling, however, also presents difficulties – accuracy and precision in parameter estimation, oversimplification and validity testing, to mention the most obvious – but it does provide a tractable

methodological framework for analysis, some predictive value and suggestions for further experimental work. As no approach is free of problems, it is through the integration of different methodologies that one may hope to make progress in the analysis of large-scale patterns and drivers of biodiversity.

The ability to integrate modeling, correlative and experimental approaches within individual research programs is therefore a new frontier in the analysis of large-scale, long-term environmental problems. Scale-transition theory (STT) enables this level of integration, providing a powerful framework to link ecological patterns and processes across scales (Chesson et al., 2005; Melbourne et al., 2005; Melbourne and Chesson, 2006) [see also Sears and Chesson (Sears and Chesson, 2007) and Angert et al. (Angert et al., 2009) for applications of STT in the context of species coexistence]. STT predicts the large-scale (e.g. regional) behavior of a system on the basis of the interaction between nonlinear population processes driving local (e.g. patch-scale) population dynamics and spatial variation in population abundance or environmental conditions. Once the local model is identified, the parameters that determine nonlinearities at the local scale are estimated from experimental data and combined with the relevant components of spatial variation estimated from sampling programs to obtain the scale transition (e.g. Melbourne and Chesson, 2006).

The key concept behind STT is nonlinear averaging – i.e. the averaging of nonlinear functions. We know from basic statistical principles that averaging the values of a quantity over a sample of observations collected at a particular scale enables one to estimate the mean value of the quantity at the larger scale defined by the statistical population that has originated the sample (e.g. Stuart and Ord, 1994). Similarly, one can represent the dynamics of a population at the regional scale by averaging a model for local dynamics over a number of replicate patches. Special care is required when averaging nonlinear functions, however, because the function of the average is generally different from the average of the function in the nonlinear scenario. An example of nonlinear averaging that has been discussed to some extent in ecology is Jensen's inequality (Jensen, 1906; Chesson, 1991; Ruel and Ayers, 1999; Benedetti-Cecchi, 2005). Nonlinear averaging can be performed through quadratic approximation, which involves the product between the second derivative of the function (quantifying the strength of the nonlinearity) and the variance associated with the focal variable (e.g. population abundance) (Chesson et al., 2005).

We used STT to predict the dynamics of turf-forming macroalgal assemblages of rocky shores at Capraia Island, in the northwest Mediterranean. Many algal-dominated marine ecosystems around the globe are undergoing major shifts, with highly productive algal canopies being replaced by less-productive turf-forming assemblages, apparently in response to increasing levels of nutrient and sediment loads (Benedetti-Cecchi et al., 2001; Airoldi, 2003). We developed a model of algal turf dynamics based on density-dependent growth that included the effects of local interactions with *Cystoseira amentacea* Bory var. *stricta* Montagne, a perennial canopy alga. The model was parameterized with field data and used to scale up the dynamics of algal turfs from the scale of the plot (20×20 cm) to the island scale (tens of km). Model predictions were then compared with observed values of mean turf cover obtained independently from a separate experiment. We found that the model was able to predict both short-term and long-term mean values of turf cover at the island scale. Motivated by this positive outcome, we conclude by highlighting the connections between STT and biomechanics, the theme of this Special Issue of JEB.

Materials and methods
Applying STT
A local model for algal dynamics

We start from a general model describing algal turf dynamics at the scale of the individual plot x within patches of *C. amentacea*:

$$\frac{dT_x}{dt} = G(T_x) - H(T_x)C_x + R(T_x) - M(T_x) , \qquad (1)$$

where T_x is the percentage cover of algal turfs, t is time and C_x is the percentage cover of *C. amentacea*. The function $G(T_x)$ describes the rate of growth of algal turfs and $H(T_x)C_x$ reflects the rate of competitive exclusion of turfs by *C. amentacea* (both rates are expressed as percentage cover per unit of time). The generic function $R(T_x)$ describes turf recruitment (i.e. the recruitment of the species composing the turf), whereas $M(T_x)$ reflects turf mortality due to physical disturbance (e.g. dislodgement by waves and desiccation). Grazing is not considered as a source of mortality for algal turfs, as herbivores are generally rare in the habitat dominated by *C. amentacea* (Benedetti-Cecchi et al., 2001).

The recruitment and mortality terms in Eqn 1 may be expanded to include additional ecological processes. For example, the generic function $R(T_x)$ could include any form of propagule production, dispersal and settlement as a function of available space. One might also include a term to reflect recruitment inhibition of turf by *C. amentacea*. For example, a term such as $R(100–T_x–C_x)$ might be used to model turf recruitment as a function of the percentage cover of unoccupied space. Being specific about the precise form of a term is important as far as nonlinearities are involved, but linear terms play no role in the scaling-up process. We currently lack the appropriate data to be more specific about the recruitment and mortality terms and to decide whether they should be linear or nonlinear. However, as we will detail in the next section (see below, Scaling up the local model), we have reasons to suspect that they will offset each other at the island scale, so these terms will not appear in the scaled-up model.

To fully describe the turf–*Cystoseira* system, one should couple Eqn 1 with a model for *C. amentacea* dynamics. However, the dynamics of *C. amentacea* are slow compared with those of the algal turfs, so we assume that at the time scales relevant to this study (months to years) and at the spatial scale of the island (the scale at which we want to translate the local dynamics of algal turfs), the average change in cover of *C. amentacea* is effectively zero. This assumption is justified by long-term observations indicating negligible changes in average percentage cover of *C. amentacea* at Capraia Island over a period of 15 years (L.B.-C., unpublished data). Assuming constant average cover for *C. amentacea* may, however, obscure the effect of seasonal fluctuations in canopy abundance on turf dynamics, an issue that we will address in the Discussion.

Scaling-up the local model

We used STT to scale up the local model of algal turfs to the island scale, where individual plots are linked by propagule dispersal. The dynamics at the island scale are obtained by taking averages of both sides of Eqn 1:

$$\frac{d\overline{T}}{dt} = \overline{G(T)} - \overline{H(T)C} + \overline{R(T)} - \overline{M(T)} . \qquad (2)$$

More than 15 years of observations and quantitative sampling (L.B.-C., unpublished data) at Capraia Island suggest that an equilibrium for mean algal turf cover (T) has been reached and maintained at the island level, despite local variation. We therefore

assumed that the stochastic processes of recruitment and disturbance were temporally stationary at the island scale, their density-dependent interaction leading to a balance between gains and losses of algal turfs. The growth and competition terms of Eqn 2 are, in contrast, subject to the effects of variance.

If these assumptions hold, then $\overline{R(T)}-\overline{M(T)}=0$ and the dynamics at the island scale become:

$$\frac{d\overline{T}}{dt} = \overline{G(T)} - \overline{H(T)C} \ , \tag{3}$$

where $\overline{G(T)}$ and $\overline{H(T)C}$ are the averages of functions G and H over turf and *C. amentacea* cover, respectively. If G and H were linear functions, one could express the average dynamics of algal turfs at the island scale simply as a function of the average values of variables T_x and C_x – i.e. the mean field model $G(\overline{T})-H(\overline{T})\overline{C}$. This scenario is, however, unrealistic. Density-dependent processes are known to result in nonlinear patterns of population growth and to generate nonlinear outcomes of competitive interactions (Royama, 1992). Therefore, describing the average dynamics of algal turfs simply as a function of the averages of variables T_x and C_x would be misleading. STT addresses this problem by correcting the mean-field model with the inclusion of appropriate scale-transition terms:

$$\frac{d\overline{T}}{dt} = \underbrace{G(\overline{T}) - H(\overline{T})\overline{C}}_{\text{mean-field model}} + \underbrace{S_G - S_H\overline{C} - S_{HC}}_{\text{scale-transition terms}} \ , \tag{4}$$

where S_G and $S_H\overline{C}$ correct for nonlinearity in turf growth and competition with *C. amentacea*, respectively, and S_{HC} arises because the competitive effect of *C. amentacea* is the product of canopy cover and rate of turf growth. The scale-transition terms are approximated by second-order Taylor expansion of $G(T_x)$ and $H(T_x)$, such that:

$$\overline{G(T)} \approx G(\overline{T})+\frac{1}{2}G''(\overline{T})Var(T) \ , \tag{5}$$

and

$$\overline{H(T)C} \approx H(\overline{T})\overline{C}+\frac{1}{2}H''(\overline{T})Var(T)\overline{C}+H'(\overline{T})Cov(T,C) \ , \tag{6}$$

[see general formulae in Chesson et al. (Chesson et al., 2005)]. Hence, Eqn 4 becomes:

$$\frac{d\overline{T}}{dt} = \underbrace{G(\overline{T}) - H(\overline{T})\overline{C}}_{\text{mean-field model}}$$
$$+\underbrace{\frac{1}{2}G''(\overline{T})Var(T)-\frac{1}{2}H''(\overline{T})Var(T)\overline{C}-H'(\overline{T})Cov(T,C)}_{\text{scale-transition terms}}. \tag{7}$$

This approximation shows that the discrepancy between predictions based on the mean field model and the actual dynamics of turf cover at the island scale are the result of interactions between nonlinear processes and spatial (co)variation in abundance of algal turfs and *C. amentacea*. The sign of the second derivatives $G''(\overline{T})$ and $H''(\overline{T})$, which is positive if these functions are concave-up or negative if they are concave-down, determines whether the first two scale-transition terms dampen or amplify the effect of spatial variance on turf dynamics at the island scale. *Cystoseira amentacea* affects turf dynamics indirectly, through spatial covariation with turf cover. The size and direction of this effect depends on the sign of the first derivative $H'(\overline{T})$ and the sign and magnitude of the covariance between canopy and turf cover. Eqn 7 identifies the

relevant quantities that need to be measured empirically to scale up the local model of turf dynamics at the island scale. These include experimental data to select local models for turf growth and competition with *C. amentacea* [functions $G(T_x)$ and $H(T_x)C_x$ in Eqn 1], along with the nonlinearities expressed by the second derivatives of these functions, and sampling data to estimate spatial variance in turf cover and the covariance between turf and *C. amentacea* cover.

Data collection and model processing
Study system
All empirical data were collected on the rocky shores of Capraia Island (43°02′4″N, 9°49′09″E) in the Tuscany Archipelago (northwest Mediterranean) between 1999 and 2010. In many places around the island, the lowshore habitat (0 to –0.3 m with respect to the mean low level water) is occupied by extensive belts of *C. amentacea*, a perennial alga that forms a canopy 30–40 cm high. A removal experiment showed that *C. amentacea* is responsible for maintaining a rich assemblage of invertebrates (mainly sponges and hydrozoans) and understory algae, while preventing the colonization of algal turfs (Benedetti-Cecchi et al., 2001). The algal turf category includes several species of coarsely branched and articulated coralline algae that are generally abundant below the belt of *C. amentacea*, but that massively colonize the upper shore level only in the absence of canopy algae (Bulleri et al., 2002).

Specific functions for turf growth and competitive exclusion
We formulated three alternative models for each of the growth and competitive functions in Eqn 1 (Table 1). Candidate models for turf growth included Gompertz, logistic and exponential functions. The first two are classical continuous models with density-dependence regulation leading to nonlinear dynamics (Royama, 1992; Lande et al., 2003). The exponential function implied linear rates of population change and was used for reference: scale-transition terms would disappear from Eqn 7 if functions were linear, in which case the mean field model would be appropriate to describe turf dynamics at the island scale.

The rate of competitive exclusion of algal turfs by *C. amentacea* was modeled through bump-exponential, exponential-decay and linear functions. The bump-exponential function would be appropriate if, for example, the rate of competitive exclusion increased with increasing turf cover up to a threshold level, decreasing thereafter. This pattern would be consistent with the view that the outcome of asymmetric competitive interactions may be reversed depending on the relative abundance or ontogenetic status of interacting species (e.g. Lawler and Morin, 1993; Benedetti-Cecchi, 2000). The exponential-decay function, in contrast, would be more appropriate to model nonlinear competitive outcomes in the absence of competitive reversals. Finally, we included the linear function for reference.

Field data: canopy removal experiment and hierarchical sampling design
We fitted the local models for turf growth and rate of competitive exclusion to empirical data from a canopy removal experiment and a hierarchical sampling design, respectively. The experiment consisted of removing the fronds and bases of *C. amentacea* with a hammer and chisel from areas of shore of 2×0.5 m (the longer axis was in the alongshore direction). Inevitably, the algae and invertebrates epiphytic on *C. amentacea* were also removed, but we paid attention to minimize the damage to organisms attached to the primary substratum, including algal turfs. In May 2000 we

Table 1. Models for growth of algal turfs and competitive exclusion rate by *Cystoseira amentacea*

Model	Formula	Parameters
Turf growth		
Gompertz	$G(T_x)=rT_x(\log K - \log T_x)$	r, density-independent growth rate K, carrying capacity
Logistic	$G(T_x)=rT_x[1-(T_x/K)]$	
Exponential growth	$G(T_x)=rT_x$	
***C. amentacea* competition**		
Bump-exponential	$H(T_x)C_x=aT_x e^{bT_x}C_x$	a, asymptotic competitive exclusion rate when turf cover approaches zero b, exponential parameter for competitive exclusion rate
Exponential-decay	$H(T_x)C_x=ae^{bT_x}C_x$	
Linear	$H(T_x)C_x=aT_x C_x$	a, linear parameter for competitive exclusion rate

marked with epoxy putty (Subcoat S, Veneziani, Trieste, Italy) the corners of nine areas on each of two shores (stretches of coast 30–50 m in length) approximately 1 km apart. Three replicate areas were randomly allocated to each of three starting dates of the experiment on each shore: May 2000, October 2000 and December 2001. Thus, each shore had three experimental areas cleared at three times over a period of 1.5 years; this experimental design enabled us to assess turf growth in the absence of *C. amentacea* over a range of starting environmental conditions. Percentage cover of algal turfs was measured soon after clearing and 6 months later in three plots of 20×20 cm marked in each area, using standard sampling procedures (Benedetti-Cecchi et al., 2001).

Three unmanipulated areas of the same size as the cleared ones were also established at each date on each shore as controls. Because this experiment was designed primarily to examine the effect of removing a dominant canopy alga on other species in the assemblage, we stratified the experiment on shores that had a full cover of *C. amentacea*. As a result, algal turfs were rare in these control areas, so that the range of initial values of turf and *C. amentacea* cover was too narrow for model fitting and parameter estimation (see Model selection and parameter estimation).

As an alternative, we used data from a hierarchical sampling design that was also employed to estimate spatial variances and covariances. On eight occasions between September 1999 and July 2004 we sampled nine shores (stretches of coast 30–50 m in extent) distributed around the island of Capraia at distances of 0.2 to 10 km. At each sampling date, two areas of the same size as those used in the clearing experiment were selected on each shore and five replicate plots of 20×20 cm were sampled in each area. All sources of variation were random in the sampling design. Data from the same shore at two sampling occasions were necessary for selecting a local model of competitive interactions between *C. amentacea* and algal turfs (see Model selection and parameter estimation). We used data from the first and the fourth sampling date of the hierarchical sampling design (September 1999 and December 2000), which provided the best compromise in terms of overlap and duration with respect to the canopy removal experiment.

Model selection and parameter estimation
We fitted the alternative models of turf growth $G(T_x)$ and competitive exclusion $H(T_x)C_x$ to final values of turf cover obtained from the canopy removal experiment and hierarchical sampling design, respectively, using maximum likelihood procedures. To obtain predicted values of final turf cover, we integrated initial values through time using the lsoda function of the odesovle package in R 2.10 (R Development Core Team, 2010). Models for turf growth were fitted to turf cover data from individual plots sampled within areas cleared of *C. amentacea*. Models for the exclusion rate of turfs by *C. amentacea* were fitted to final turf

cover data averaged at the shore scale, using average canopy cover as a covariate and $G(T_x)$ set to the best-fitting model among the candidate models estimated from the canopy removal experiment. We used shore averages of turf cover for this analysis because sampling areas differed among dates in the hierarchical design (i.e. areas were nested within shore × sampling date combinations), so only data aggregated at the shore level could be tracked through time. We evaluated the support of the data to the alternative models for turf growth and *C. amentacea* competition through the bias-corrected Akaike's information criterion (AIC_c) (Burnham and Anderson, 2002). Likelihood profiles were inspected to ensure that parameters were well defined.

The fitting procedure assumed that the initial values of turf cover were estimated without observation error and that all the error was in the final values. Observation error in the initial values resulted in biased estimates of model parameters (Melbourne and Chesson, 2006; Bolker, 2008). To correct for this bias, we used the simulation–extrapolation (SIMEX) method (Cook and Stefanski, 1994). This method is based on Monte Carlo simulations where new data sets are generated by contaminating the original data (the initial values of turf cover in our case) with known amounts of observation error, so to increase the total variance of the simulated series. Model parameters are estimated for data sets with increasing levels of observation error and regression procedures (e.g. quadratic regression) are used to relate each parameter to total variance. Bias-corrected estimates of the parameters are then obtained by extrapolating the regressions to zero variance (i.e. zero observation error). We used the SIMEX method to correct parameter estimates for selected models of turf growth and competitive exclusion. To apply the SIMEX procedure, one must have an independent estimate of observation error. We obtained such estimates from the variance component analysis described in the next section, using variances at the plot scale for the growth model and the compound variance at the plot and area scales for the competition model, thereby accounting for the error introduced by using turf cover data aggregated at the shore level when selecting a function for competitive exclusion.

Estimating spatial variances and covariances
To apply the scale-transition model, we needed estimates of the variance and covariance components appearing in Eqn 7. The hierarchical sampling design enabled us to estimate spatial variances in turf cover and covariances between turf and *C. amentacea* cover at three spatial scales: among plots within sites, among sites within shore × sampling date combinations, and among shores (i.e. the island scale). We used the subset of sampling dates also employed to select the local model of competitive exclusion for this analysis (from September 1999 to December 2000). In this way variances and covariances were estimated on a time scale comparable to that used to select growth and competitive functions.

Variance components were estimated through restricted maximum likelihood using the function lmer in the lme4 package of R 2.10 (R Development Core Team, 2010). Covariance components were estimated at each spatial scale as half the difference between the variance of the sum of turf and *C. amentacea* cover and the sum of the variance components of the individual variables (Searle et al., 1992). The relevant quantities to plug into Eqn 7 were the total variance in turf cover and the total covariance between turf and *C. amentacea* cover, each obtained by summing the corresponding (co)variance components across the three spatial scales examined. Analyses were performed on untransformed data.

Quantifying the scale transition and testing predictions

We assessed the contribution of each scale-transition term in Eqn 7 as the change caused by a focal term to the instantaneous rate of change of turf cover with respect to the mean field model. We also tested whether the model was able to predict short-term and long-term mean values of turf cover when applied to a new scenario. The extent to which a scale-transition model can be used for predictions beyond instantaneous rates of change depends on the underlying assumptions, the ability to obtain spatial variances and covariances as a function of a wide range of mean values of the focal variable, and the time scales at which variances and covariances are estimated (Melbourne and Chesson, 2006). This last point is of great concern when extending the predictions of a scale-transition model, as spatial variances and covariances are dynamic quantities, so estimates based on a single sampling occasion may not be adequate for long-term predictions (Melbourne and Chesson, 2006; Englund and Leonardsson, 2008). Our main assumptions of constant average cover of *C. amentacea* and zero-sum dynamics of turf recruitment and mortality at the island scale were reasonable for time scales of years. Furthermore, because our hierarchical sampling design extended over several years, we could estimate mean-variance/covariance relationships empirically and use these relationships to find the scale-transition terms in Eqn 7. We estimated the variance in turf cover and the covariance with *C. amentacea* at the scales of plot, area and shore for each year separately. We obtained eight data points, one for each year, of the following quantities: mean and variance of turf cover, mean *C. amentacea* cover and the covariance between turf and canopy cover (with variances and covariances summed across the three spatial scales examined). Ordinary least squares regression was then applied to predict spatial variance of turfs as a function of mean cover and spatial covariance as a function of mean cover of both algal turfs and *C. amentacea*.

The new scenario used to test predictions originated from an additional experiment in which *C. amentacea* was manipulated along transects of 64 quadrats of 0.5×0.5 m arranged in the alongshore direction. The experiment started in June 2006 as part of a larger study on the response of *C. amentacea* assemblages to multiple disturbances characterized by different levels of spatial autocorrelation. To assess the predictions of the scale-transition model, we used a subset of available experimental treatments, consisting of four transects marked on shores 0.1 to 10 km apart (one transect per shore). The canopy of *C. amentacea* was clipped in half the quadrats along each transect once a year (at some point between February and April) until 2010. The aim of this treatment was to impose a spatially autocorrelated disturbance (with a known level of autocorrelation), so each transect consisted of series of quadrats subjected to clipping interspersed among unclipped quadrats in the alongshore direction. The occurrence of patches of

C. amentacea with a reduced canopy among areas with fully developed fronds is a natural, highly autocorrelated spatial pattern on some shores (data not shown). Canopy loss may be a consequence of senescence, heavy storms or a combination of these events. Two of the four transects had an additional treatment, consisting of small clearings of 5×5 cm distributed randomly along the transect. Clearings were produced by removing all attached organisms from the substratum with a hammer and chisel. Approximately 12% of the total area of each transect was disturbed in this way. This treatment mimicked the effects of episodic extreme storms, producing small gaps of cleared space within algal-dominated assemblages. Field measurements not reported here have shown that the spatial distribution of these gaps is nearly random. The rationale behind these experimental treatments is not particularly important for the purpose of testing the scale-transition model. The key point is that these treatments (hereafter called the transect experiment) provided a novel context in terms of mean cover of algal turfs and *C. amentacea* and related spatial variances and covariances that differed from the one used to select the growth and competitive functions of the model.

We were interested in determining whether the scale-transition model was able to predict the equilibrium abundance of algal turfs when applied to the new scenario defined by the transect experiment. Equilibrium abundance, $\bar{T}^*$, was defined as the percentage cover that algal turfs attained when growth rate matched the rate of competitive displacement at the island scale – i.e. when $d\bar{T}/dt=0$. We compared the predictions of the mean field model and the full model over the range of mean turf cover ($\bar{T}$ in Eqn 7) from 1 to 100, with the mean cover of *C. amentacea* set to the value estimated at the first sampling date of the transect experiment, which was in January 2007, 7 months after the start of the experiment. The variance and covariance terms to plug into Eqn 7 were obtained from the mean-variance/covariance relationships described above. Predictions were compared with estimates of mean turf cover obtained by sampling the transect experiment after 1 year (short-term prediction) and 4 years (long-term prediction). In each case, the mean values of turf cover were obtained by stratified bootstrapping of the observed data within transects, with 999 replicates. This enabled us to associate bias-corrected confidence intervals with estimated means (Davison and Hinkley, 1997).

Results and discussion

Data from the canopy removal experiment provided very similar support to the Gompertz and logistic models of turf growth, and these models were favored over exponential growth, which received little support (Table 2). AIC_c was slightly lower for the Gompertz model, so we selected this growth function for subsequent analysis. SIMEX-corrected parameter estimates for the Gompertz model were $r=0.148$ month^{-1} and $K=98.7\%$ cover; we used these parameters to fit the model to the experimental data (Fig. 1A).

Control data from the hierarchical sampling design provided nearly equal support to the exponential-decay and the bump-exponential models, whereas the linear model did not converge (Table 2). Based on AIC_c values, we selected the exponential-decay function to model the rate of turf exclusion from competition with *C. amentacea* (Table 2). The exponential parameter was negative, indicating that the rate of competitive exclusion decreased with increasing cover of algal turfs. When corrected with the SIMEX procedure, parameter estimates for the exponential model were $a=0.089$ (turf cover^{-1} *C. amentacea* cover^{-1} month^{-1}) and $b=-0.0067$ (turf cover^{-1}). We used these parameters to fit the

Table 2. *Parameter estimates, negative log-likelihood (L) and bias-corrected Akaike's information criterion (AIC$_c$) for local models of turf growth and C. amentacea exclusion rate*

Model	Parameter estimates (units)	L	AIC$_c$
Turf growth			
Gompertz	K=86.9 (% cover) r=0.144 (month^{-1})	43.74	91.8
Logistic	K=58.9 (% cover) r=0.380 (month^{-1})	43.76	91.9
Exponential growth	r=0.159 (month^{-1})	53.72	111.8
C. amentacea competition			
Bump-exponential	a=7.8×10^{-3} (month^{-1} C^{-1}) b=−3.7×10^{-2} (month^{-1} T^{-1})	48.5	103.0
Exponential-decay	a=0.0879 (month^{-1} $T^{-1}C^{-1}$) b=−0.00765 (T^{-1})	48.1	102.2
Linear	Convergence problems		

C, percentage cover of *C. amentacea*; T, percentage cover of turf.

exponential-decay model to control data, with growth set to the parameters of the Gompertz model (Fig. 1B).

A potential problem with the exponential-decay model for competitive exclusion is that the model predicts a positive exclusion rate (through parameter a) for zero turf cover, which does not make sense. We feel that this is not a substantial problem when using the exponential-decay model in combination with the Gompertz growth function, which has meaning only for positive values of turf cover. That is, the natural extension of the Gompertz function to $G(0)$=0 does not change the substance of the analysis, which takes place in the range T>10.

Using data from the first four dates of the hierarchical sampling design (from September 1999 to December 2000), we obtained an estimate of the spatial variance of turf cover at the island scale of 879, whereas spatial covariance between turf and *C. amentacea* cover was −665. Mean values of turf and *C. amentacea* cover were 35 and 33%, respectively. We emphasize that these estimates came from a sampling design that included shores with fully developed canopies and shores where canopy cover was sparse; this provided a wide range of abundances of algal turfs and *C. amentacea*, which was necessary for model parameterization. Thus, these data did not reflect the abundance of algal turfs in the presence of fully developed canopies of *C. amentacea*, but they provided our best estimates of the mean cover of these algae at the island scale.

Applying these mean and (co)variance estimates to Eqn 7 and combining the Gompertz model of turf growth with the exponential function for competitive exclusion, we obtained the scale transition for the instantaneous rate of change of turf cover (d$\bar{T}$/dt). Although the mean field model predicted an instantaneous rate of change of 3.03 units of percentage cover per month at the plot scale, the full

model including the scale transition terms predicted a rate of change of 0.83 units of percentage cover per month. Thus, the interaction between nonlinearity and spatial (co)variance reduced d$\bar{T}$/dt at the island scale by 73%.

The term that contributed the most to this scale transition was S_G, whereas the contribution of the term S_HC was negligible (Fig. 2). This was a consequence of the strong nonlinearity in turf growth and the large spatial variance in turf cover. Nonlinearity in turf growth [term $G''(T)$ in Eqn 7] was −0.0042, more than three orders of magnitude larger in absolute value than the nonlinearity in competitive exclusion [term $H''(T)$ in Eqn 7], which was 3.16×10^{-6}. The term S_{HC} contributed 14% of the total change due to the scale transition. This effect resulted from the product of the first derivative of the exponential function for competitive exclusion [term $H'(T)$ in Eqn 7], which was −4.7×10^{-4}, and the covariance between turf and *C. amentacea* cover.

When applied to the transect experiment scenario, the scale-transition model displayed two non-zero equilibrium values of mean turf cover: 12.3 and 80.8% for the mean field model at the plot scale and 28.5 and 55% for the full model at the island scale. Thus, the interaction between nonlinearity and spatial (co)variance increased the lower equilibrium value of turf cover with respect to the mean field model, while decreasing equilibrium towards the upper end of the spectrum of mean cover values. Assuming equilibrium, the model correctly predicted the short-term (1 year) and long-term (4 years) mean values of turf cover from the transect experiment (Fig. 3). The confidence intervals of both short-term and long-term means embraced the island-scale model, although the mean field model was also within the confidence intervals of the short-term mean (Fig. 3). This analysis showed how the
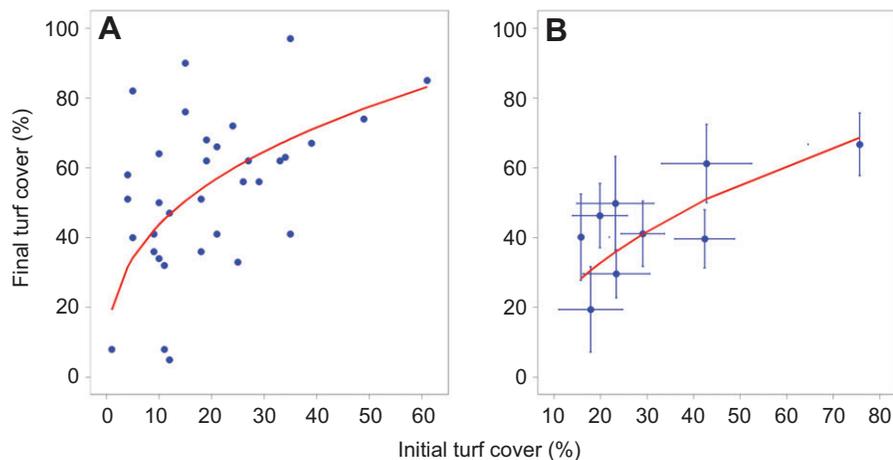

Fig. 1. Initial and final values of turf cover from individual plots cleared of *Cystoseira amentacea* (A) and as shore averages from the hierarchical sampling design obtained in September 1999 and December 2000 (B). Fitted curves are the Gompertz model of turf growth in the absence of *C. amentacea* (A) and the combination of the Gompertz model of growth with the exponential function of competitive exclusion rate in the presence of canopy algae (B). Error bars in B originated from five replicate plots pooled across two sampling areas on each shore at each sampling date.
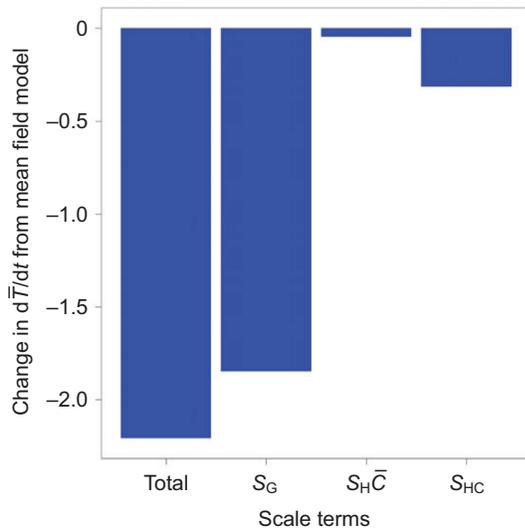
Fig. 2. Contribution of each scale transition term to the total change in the instantaneous rate of turf growth at the island scale (Eqn 4) relative to the mean field model.
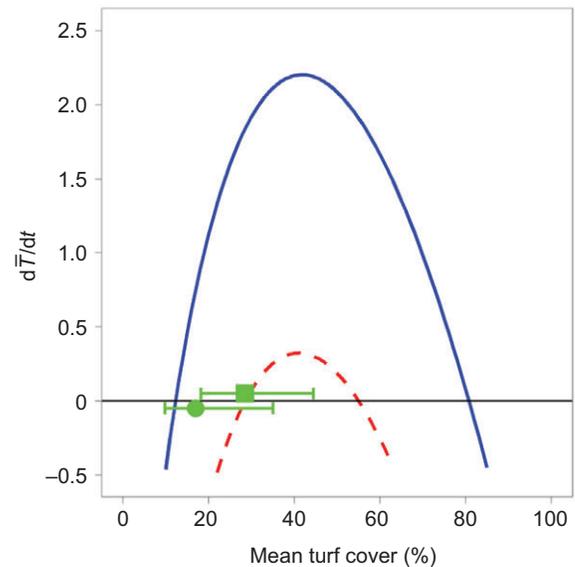

Fig. 3. Predictions from the mean-field (solid blue line) and full (red dashed line) scale-transition models applied to data from the transect experiment. Spatial variance in turf cover and the covariance with *C. amentacea* cover for scale-transition terms in Eqn 7 were obtained using mean-variance/covariance relationships estimated from the full hierarchical sampling design. The average cover of *C. amentacea* for the competition function in Eqn 7 was estimated by sampling the transect experiment in January 2007, 7 months from the start. Predictions were compared with mean values of turf cover estimated from the transect experiment after 1 year (solid circle, short-term prediction) and 4 years (solid square, long-term prediction). Error bars are 95% bias-corrected confidence intervals obtained from stratified bootstrapping of sampled data within transects (n=999).

interaction between nonlinearity and spatial (co)variance restricted the range of abundances at which algal turfs displayed positive growth rates, in addition to confirming the large impact of this interaction on instantaneous rates of turf growth at the island scale.

It is worth noting, however, that the lower equilibrium point of the scale-transition model was unstable (Fig. 3). Hence, an alternative interpretation for our results is that mean turf cover lies 'on the line' of the scale-transition model without reaching a stable equilibrium. This possibly reflects a tension between the propensity of algal turfs to grow in response to our experimental manipulations (reduction of *C. amentacea* cover and increased availability of open space for colonization) and the impact that the interaction between nonlinearity and spatial (co)variance had on instantaneous rates of turf growth. Given this tension, one may expect only small fluctuations in turf cover through time, which will be much smaller at the island scale compared with the plot scale.

Collectively, our results have important implications for the ability of algal turfs to spread in the *C. amentacea* habitat and to persist high on the shore at Capraia Island. Predictions from the scale-transition model suggest that algal turfs may be near a critical threshold of low abundance, where any further reduction in mean cover may push dynamics towards a region of negative growth, possibly leading to extinction from the *C. amentacea* habitat (Fig. 3). Our long-term observational and experimental data suggest that this should not be the case until there are areas of shore free of canopies that algal turfs can colonize. However, all scaling terms operated in the direction of reducing turf growth rates, so the compound effect of these terms makes any increase in mean cover of algal turfs unlikely in the *C. amentacea* habitat.

Our analysis also disclosed a previously unrecognized mechanism that may help explain how algal turfs respond to a massive loss of canopy algae. Extensive belts of *C. amentacea* maintained large spatial variance of turf cover by inhibiting their recruitment and induced strong negative covariance with algal canopies at the island scale. As we have seen, these terms interacted with nonlinearity to depress turf growth. These interactions would become much less important if canopy algae disappeared from large areas because algal turfs would face a more homogeneous

environment. Hence, mitigation of spatial (co)variances may amplify the positive effect of canopy loss on turf recruitment. This mechanism may account for the ability of algal turfs to replace canopy algae, a shift in dominance that seems to be triggered by anthropogenic disturbance and to occur on many rocky shores around the globe (Benedetti-Cecchi et al., 2001; Gorgula and Connell, 2004; Airoldi, 2003; Mangialaio et al., 2008).

As always with models, the accuracy of predictions depends on the validity of the underlying assumptions. We assumed constant mean cover of *C. amentacea* at the island scale, an assumption supported by our long-term observations for spring and summer months, when canopies are fully developed. However, *C. amentacea* undergoes seasonal dynamics driven by the loss of secondary fronds after the reproductive period, which results in reduced canopy cover in fall and early winter (L.B.-C., personal observation). The consequences of these seasonal dynamics for turf–canopy interactions remain unknown. It may be the case that canopy loss increases the substratum available for turf colonization in fall and winter, thereby contributing to the persistence of algal turfs at the island scale. This possibility requires further investigation.

For predictive purposes, we also assumed that mean turf cover was at equilibrium at the island scale. This assumption depends on whether one can consider the island as a closed system with respect to turf reproduction and dispersal. Capraia is located approximately 17 nautical miles from Corsica, the nearest piece of land and approximately 18 nautical miles from Elba, the nearest island of the Tuscany Archipelago. Although currents can certainly link

populations of benthic organisms at these spatial scales, whether this is the case for algal turfs depends on how long propagules and fragments of these algae can survive in the water column. This is currently unknown. One can assume equilibrium only if any external input of algal turfs is negligible compared with local reproduction and dispersal at time scales of months to years, the temporal horizon of our predictions.

Conclusions

Our study adds to the limited, albeit growing body of empirical evidence indicating how STT can be used to identify the relevant mechanisms that drive large-scale changes in natural populations (Bergström et al., 2006; Melbourne and Chesson, 2006; Englund and Leonardsson, 2008). This approach can be extended to scale up processes across a broad range of levels of biological and ecological organization. Specifically, we argue that STT can contribute significantly to the connection between biomechanics and ecology, a synthesis that is at the core of the emerging field of ecomechanics (Denny and Helmuth, 2009) and the central theme of this Special Issue. For example, using mechanistic models to describe population dynamics, such as bioenergetic models (reviewed by Nisbet et al., 2012), it would be possible to ground the scaling-up process into a solid understanding of the biomechanics and physiology of individual organisms. Similarly, one could build on mechanistic models to determine how the biomechanics underlying competitive or consumer–resource interactions (e.g. Baskett, 2012) translate local processes into large-scale population dynamics.

Thus, as far as nonlinear response functions are involved, STT can be used to scale up physiological to community-level processes (Denny and Benedetti-Cecchi, 2012). This flexibility reflects the generality of the key concept behind STT – the interaction between nonlinearity and spatial (co)variance. An example of how widely nonlinear averaging applies when modeling dynamical biological processes is provided by the paper of Crimaldi (Crimaldi, 2012) on gamete dispersal and aggregation in broadcast spawning. Fertilization rates in spawning organisms depend on the concentration of gametes released in the water column and can be modeled as a nonlinear function of these concentrations. However, modeling fertilization simply as a function of the mean concentration of gametes misses the fundamental mechanism responsible for their aggregation: the spatial correlation imposed by fluid dynamics on sperm and eggs. To capture this effect, it is necessary to include in the fertilization model terms that reflect fluctuations in gamete concentrations around their mean values. This example illustrates once again how the interaction between nonlinearity (in instantaneous gamete concentrations) and spatial variation (due to flow flumes in the water column) contributes to translate local dynamics (gamete production and release) into large-scale patterns (gamete aggregations).

Building on these general principles, STT will provide a powerful tool to connect individual-, population- and community-level dynamic processes across ecological scales, fostering our understanding of natural and anthropogenically induced changes in large-scale biodiversity.

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