

From habitat geometry to ecosystem functions in marine mussel beds

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ABSTRACT: Habitat geometry, especially when resulting from ecosystem-engineering species, is a key property of natural ecosystems. Habitat geometry influences the abundance and distribution of species through an interplay between habitat area and perimeter. However, few studies have tested the interacting effects of these distinct geometry parameters on community and ecosystem dynamics. We used experimental mussel (*Mytilus* spp.) beds as a model system to control and test for the effect of perimeter, area and their interaction on the diversity and abundance of macro-invertebrate species associated with mussel beds and on ecosystem functions (ammonium and oxygen fluxes). Live blue mussels were used to create artificial mussel transplants corresponding to 9 factorial combinations of area and perimeter, and both community and ecosystem effects were assessed after a 2 mo colonization period in the field. Our results showed an interacting and scale-dependent effect of area and perimeter on both community and ecosystem characteristics: area had a negative effect on taxonomic diversity of small-perimeter transplants, and perimeter had a negative effect on diversity of small-area transplants. At the ecosystem level, ammonium release increased with area in large-perimeter transplants. This study stresses the importance of integrating the explicit and interactive effects of multiple metrics of habitat shape for resolving the relationship between community dynamics and ecosystem functions in fragmented habitats.

KEY WORDS: Habitat shape · Area · Edge effect · Biodiversity · Ecosystem function · Functional groups · Nutrient fluxes · Mussels · *Mytilus* spp.

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1. INTRODUCTION

Landscape ecology is increasingly applied to marine environments to gain a better understanding of the consequences of habitat configuration, including its geometry, and fragmentation (Boström et al. 2011). Knowledge of ecosystem responses to seascape configuration has important implications for the management of coastal resources (e.g. Mizerek et al. 2011, Green et al. 2012), especially in systems where ecosystem engineers such as mussels can have a strong and dynamic impact on habitat configuration (Petrovic & Guichard 2008, van de Koppel et al. 2008) and multiple ecosystem functions (Angelini

et al. 2015). However, studies of habitat geometry in marine systems are still scarce compared to those in terrestrial systems, and there is a need to tease apart the scale-dependent effects of multiple components of habitat geometry, such as area and perimeter. The effects of habitat geometry have the potential to scale up from individuals to whole ecosystems, but few studies have tested the effects of habitat geometry on both community structure and ecosystem functions. Here we tested for the effects of mussel bed area and perimeter on the structure of associated communities and key ecosystem functions.

The patch-matrix (or island) model of landscape cover is based on the concept of island biogeography

theory (MacArthur & Wilson 1967, Franklin & Lindenmayer 2009, Wedding et al. 2011). According to this model, a patch is defined as an area of suitable habitat, which differs from its surrounding matrix of unsuitable habitats. This model focuses on the study of biotic responses to the various attributes of the patch, such as its area, perimeter, geometric shape and isolation. Area and perimeter are main parameters characterizing the geometry of habitats and can influence the distribution of resources and taxa, and ecosystem functions (Airoldi 2003, Fletcher et al. 2007). Landscape ecology further distinguishes the perimeter, which is a linear measure of the boundary length, from the 'edge' measured as the area influenced by the adjacent environment (Baskent & Jordan 1995). Variations in perimeter and total area determine the percentage of core area and edge. In natural landscapes, this results in strong covariation among area, perimeter and edges. Mechanisms associated with each of these parameters can thus have confounding effects on ecosystems, which could explain why studies of patch geometry in marine systems have led to highly variable and inconsistent results (Boström et al. 2006). The importance of considering the distinct effect of each habitat geometry parameter and their interdependence is now recognized (Ewers et al. 2007, Barbaro et al. 2012, Carpintero & Reyes-Lopez 2014), but it has rarely been explicitly addressed in marine systems (Airoldi 2003, Jelbart et al. 2006, Arponen & Boström 2012).

Mussels of the genus *Mytilus* are ecological engineers present in great abundance on marine coasts, playing a key role in shallow coastal ecosystems by contributing to dampen wave action, clarify the water, trap sediments and facilitate pelago-benthic transfers of carbon and nutrients (Richard et al. 2007, van Leeuwen et al. 2010). Yet, very few studies in seascape ecology have been conducted on rocky shores, which constitute a major habitat for mussel bed ecosystems. Most seascape studies have been carried out in seagrass ecosystems (49%) and tidal marshes (32%), and also in coral reefs (11%) and mangroves (6%) (Boström et al. 2011). Mussels typically form mosaics of patches of various sizes and shapes controlled by both biotic (Menge 1976, Hunt & Scheibling 2001, Petrovic & Guichard 2008) and abiotic factors (Paine & Levin 1981, Hunt & Scheibling 2001) and host a great diversity of macro-invertebrates (Underwood & Chapman 1996). Changes in habitat configuration, both at the landscape and at the patch scale, may affect their associated community and ecosystem functions (Tsuchiya & Nishihira 1985, Koivisto & Westerbohm 2012, Largaespada et al.

2012). However, mechanisms associated with individual geometry metrics remain largely unresolved. Our study was conducted on an intertidal mussel bed at the individual patch scale allowing experimental control of both area and perimeter.

Population size and persistence are expected to increase with habitat area. At the community level, area can influence immigration rates and affect both taxonomic richness and abundance, as well as the diversity of resources and environmental conditions (Root 1973, Gilpin & Diamond 1976). A large patch perimeter could benefit mussels and associated species on the edges of mussel patches through access to adjacent resources and could enhance ecosystem processes (Tsuchiya & Nishihira 1985, Ries et al. 2004). We might also expect an effect of the interaction between these geometry metrics. The interacting effects of habitat area and perimeter have been studied by combining multiple geometry metrics into single integrated statistics such as the proportion of core and edge habitats, or the perimeter to area ratio (P/A). In terrestrial habitats, the edge and core area effects are recognized to have a greater influence on the community structure than the total patch area (Ewers et al. 2007, Fletcher et al. 2007, Didham & Ewers 2012). Patches with a small P/A ratio have a high percentage of core area and are more likely to present a diversity of environmental conditions that support high taxonomic richness. In mussel beds, the physical roughness of mussel shells reduces current velocity and favors higher rates of deposition of sediments and pseudofeces in core areas of patches compared to edges (Butman et al. 1994, Widdows et al. 2009). In contrast, other taxa such as suspension feeders could benefit from turbulence created along edges (Sousa 1985). The P/A ratio could also affect the relative importance of biotic and abiotic processes regulating population and community dynamics. For example, mussel beds deplete algal food from the boundary layer, leading to intra-specific competition and reduced mussel growth and metabolic activities, which increase with mussel bed core area (Newell 1990, Butman et al. 1994).

Both positive and negative edge effects have been reported in marine systems (Sousa 1984, Boström et al. 2011, Arponen & Boström 2012), but are taxon-specific. The great variation in community response to habitat geometry could be explained by antagonistic and interacting effects of individual geometry properties, which are still unresolved. The responses of communities to habitat geometry also depend on the traits of individual species or groups (Ewers & Didham 2006, Jones et al. 2015), suggesting the im-

portance of functional diversity for predicting community and ecosystem responses to habitat geometry.

Integrating community and ecosystem processes in natural landscapes can lead to great improvement in the conservation and management of natural resources (Botequilha Leitao & Ahern 2002, Pittman et al. 2011). However, few studies have considered the effects of habitat geometry on ecosystem functions. Linking community structure to ecosystem functions across complex landscapes is challenging because they both vary over a great range of spatial and temporal scales and can be controlled by multiple and distinct mechanisms associated with landscape properties (Loreau 2010). Addressing this challenge thus requires that we elucidate the individual and interacting effects of landscape properties on community and ecosystem processes. Towards this goal, we conducted controlled field experiments on experimental mussel bed patches to test the effect of patch area, patch perimeter and their interaction on community characteristics (taxonomic and functional diversity, abundance) and ecosystem functions (oxygen and ammonium fluxes) at the scale of subplots within experimental patches. Our study reveals important scale-dependent pathways linking habitat geometry to community and ecosystem processes, that can be applied to the study and management of natural systems with the explicit consideration of biogenic landscapes.

2. MATERIALS AND METHODS

2.1. Data collection

2.1.1. Study site

We conducted our experiment in a rocky intertidal area near Sainte-Flavie, on the south shore of the St. Lawrence Estuary (Quebec, Canada; see also Guichard et al. 2001, Brazeau 2009, Largaespada et al. 2012). The weak inclination and the absence of freshwater tributaries, large boulders and deep tidal pools limit potential confounding factors. The regular shoreline is exposed to wave action, semi-diurnal tide cycles and ice scouring. The average tidal range was between 1.7 and 3.7 m at the time of the study, between 24 June and 22 August 2013 (Canadian Hydrographic Service 2013). Macroalgae (*Fucus* sp.) and blue mussels (composed of *Mytilus edulis*, *M. trossulus* and hybrids, hereafter collectively termed *Mytilus* spp.) are dominant species (Archambault & Bourget 1996). A 50 m stretch was chosen as our study site be-

tween 0.7 and 1.2 m of shore elevation, where natural mussel beds covered 30 to 40% of the site. Macroalgae and all natural mussel aggregates were removed prior to the experiment. The site was selected because it was clear from topographic irregularities and >30 cm crevices, and had <20% tidal pool cover (see also Guichard et al. 2001, Brazeau 2009).

2.1.2. Mussel transplants

Experimental mussel transplants (Fig. 1) were used as habitat to control for area and perimeter. Galvanized steel grids with a mesh size of 1 cm² were used as the bottom substratum of each transplant. A thin rubber mat covered the bottom of transplants to facilitate mussel byssal attachment (Largaespada et al. 2012). A thin plastic net with a mesh size of 1 cm² covered each transplant and was attached along the bottom of each transplant to define 10 × 10 cm subunits, thus limiting changes in mussel aggregation size and shape through passive and active movement within

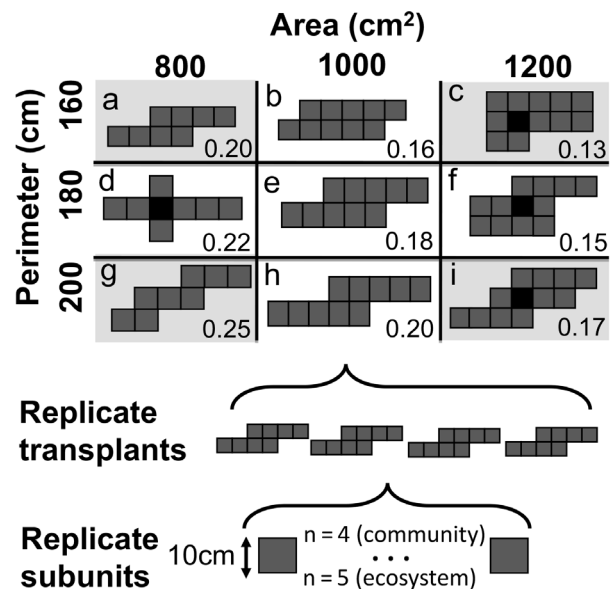


Fig. 1. Shapes of the experimental mussel transplants corresponding to the 9 combinations (a–i) of area (800, 1000, 1200 cm²) and perimeter (160, 180, 200 cm) in a factorial design. Each transplant is composed of subunits (10 × 10 cm). Values of the perimeter to area ratio (cm⁻¹) associated with each transplant are indicated in the bottom-right corners. Subunits with a central or border position are identified in black and grey, respectively. Shaded treatment levels (a, c, g, i) correspond to the subset of treatment levels used to assess oxygen and ammonium fluxes. Four replicate transplants were used for each combination of perimeter and area. Four randomly selected replicate subunits were sampled for community analysis, and 5 subunits were randomly selected for assessment of oxygen and ammonium fluxes

the transplant (Fig. 1). Although the physical structure of our subunits can affect hydrodynamics and colonization, empty subunits were previously found to have much lower abundance and number of species (4 ± 1 ; mean \pm SE) at the same study site, compared to subunits containing empty mussel shells or live mussels (19 ± 0.5 ; Largaespada et al. 2012). Live mussels between 3 and 4 cm were collected from natural mussel beds located 1.2 km downstream from the study site and rinsed with seawater to remove associated species and sediments. Mussels were then added to each transplant at a fixed density of 3000 ind. m^{-2} (30 ind. subunit $^{-1}$). In total, 36 transplants were used, corresponding to all combinations of area (800, 1000 and 1200 cm^2) and perimeter (160, 180 and 200 cm) treatment levels, according to a factorial design (Fig. 1). Multiple combinations of subunits could lead to each area and perimeter size. In order to control for geometric complexity resulting from such combinations, we increased perimeter by adopting elongated shapes. We also oriented transplants parallel to shore to limit interactions between transplant orientation and hydrodynamics, including increased wave exposure with increasing perimeter. Each combination of area and perimeter included 4 replicate transplants with identical shape (Fig. 1). Mussel transplants were left for 4 d in flow tanks supplied with unfiltered water to allow for byssus attachment. Transplants were randomly distributed at the study site, with a minimum distance of 1 m apart from each other to avoid between-transplant interactions (Brazeau 2009). All transplants were fixed on the bare rock of the study site between 24 and 26 June 2013 using stainless metal screws for a period of 56 d corresponding to the peak of the colonization period for most associated taxa (Brazeau 2009, Largaespada et al. 2012).

2.1.3. Community of associated taxa

Transplants were collected from the study site between 19 and 22 August and brought to the laboratory for analysis. We randomly selected 4 subunits from each transplant for analysis. Macro-invertebrates associated with each subunit were sampled by rinsing the mussels and the rubber mat over a 500 μm sieve and preserved in a buffered 4% solution of formaldehyde. In each subunit, live and dead mussels were counted and weighed. All macro-invertebrates were then identified under a dissecting microscope to the lowest taxonomic level possible, and the density of each taxon was evaluated. The number of individuals for each taxon was used to determine

taxonomic richness, total abundance (density) and Shannon diversity index (Pielou 1966). Density and richness of functional groups were also calculated. Each taxon was assigned to a functional group based on mode of locomotion of their adult stage (Borthagaray et al. 2009): 'swimmers' are highly mobile and can swim in the water column, 'crawlers' are mobile taxa that crawl on the substrate, and taxa with a sessile adult stage are simply referred to as 'sessile' (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m608p149_supp.pdf).

2.1.4. Ecosystem functions

Ecosystem functions were assessed by measuring ammonium and oxygen fluxes. Four replicate transplants in each of the 4 extreme combinations of area and perimeter (treatments a, c, g and i; Fig. 1) for a total of 16 transplants were used to measure oxygen consumption and ammonium release. Five subunits were randomly selected within each transplant and incubated in sterile dark 20 l chambers (27 cm diameter) made of high-density opaque polyethylene. Absence of light allowed to control for photosynthesis; thus only the processes associated with respiration activity of the overall community were studied (Hargrave 1969, Plante-Cuny et al. 1998). Mussels and their associated community were incubated together, and a single chamber was used per transplant. The chambers were previously washed with acid water (HCl 10%), rinsed abundantly and filled with unfiltered water pumped off the St. Lawrence estuary (hereafter referred to as the reference water). Each chamber, hermetically closed, contained a submersible pump that ensured water mixing. In order to avoid variations in temperature that can affect oxygen consumption from benthic communities (e.g. Upton et al. 1993, Cowan et al. 1996), chambers were installed in a network of basins supplied with circulating seawater at approximately 10°C. Ten ml of water were sampled at the beginning of the incubation, followed by 4 additional samplings every 60 min, for a total incubation time of 4 h. During each sampling, the equivalent volume of reference water was injected to keep the water volume constant in the chamber. By the end of each incubation, oxygen concentration was depleted by less than 30%, which prevents hypoxic conditions (Mazouni et al. 1996, Richard et al. 2007). Water samples were filtered on Whatman GF/F filters and directly preserved at $-20^{\circ}C$. Oxygen concentration was measured with a YSI Pro2030 probe within the chamber and the refer-

ence water at each sampling interval. Ammonium concentration was measured using ionic chromatography (Hall & Aller 1992). Fluxes of oxygen and ammonium were determined from the slopes of the linear regressions established between incubation time and concentration.

2.2. Data analysis

2.2.1. Community of associated taxa

We tested for the fixed effects 'area' (3 levels), 'perimeter' (3 levels) and their interaction on richness, total abundance and Shannon diversity index calculated at the scale of subunits, based on taxonomic and functional grouping of individuals. Following previous studies, we also tested for an effect of the P/A ratio (8 levels) (Sousa 1985, Helzer & Jelinski 1999, Arponen & Boström 2012). These analyses were performed with and without the dominant species, *Littorina* sp., which was much more abundant than any other taxon, accounting for 78% of the total density, and dominated all variations in abundance at the community level. The presence of *Littorina* sp. did not influence analysis of species richness because it was present in all subunits.

We constructed linear mixed models and generated p-values to assess the variability of community characteristics explained by habitat geometry variables using 'lme4' and 'lmerTest' in R (R Core Team 2013). Models included the fixed variables 'area' (3 levels), 'perimeter' (3 levels) and their interaction. Random effects for transplant (36 levels) were included in the model to account for within-transplant variability among subunits (Table 1). Richness, total abundance (density) and Shannon diversity index, calculated for taxa and functional groups, were used as dependent variables. The number of subunits available for community analysis was lower for small-area transplants from which subunits were incubated. This practical constraint, and the loss of 1 sample, resulted in unequal sample sizes (2, 3 or 4 subunits per transplant). Assumptions of normality and linearity were checked by visual inspections of plots of residuals against fitted values. Data of abundance (density) and richness were $\log_{10}+1$ transformed to meet the normality assumption. Bartlett's test was used to test homogeneity of variances (Snedecor & Cochran 1989). The presence of influential data points was assessed using Cook's distance (Cook 1977), and no influential point was found. Inspection of model residuals showed that negative

Table 1. P-values extracted from linear mixed effects models testing (A) the effects of area and perimeter of mussel transplants and (B) the effect of the perimeter to area (P/A) ratio on Shannon diversity index, taxonomic richness [$\log(\text{richness} + 1)$ transformed] and abundance [$\log(\text{density} + 1)$ transformed]. Transplant was included as a random variable. *Littorina* sp. was excluded from the dataset. Num: numerator; Den: denominator. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$

Source of variation	Num df	Den df	Mean square	F	p
Shannon diversity index					
A Area	2	36	0.532	3.491	0.041*
Perimeter	2	36	0.193	1.269	0.293
Area×Perimeter	4	36	0.426	2.796	0.041*
B P/A ratio	1	37	0.088	0.586	0.449
Taxonomic richness					
A Area	2	37	0.081	1.269	0.293
Perimeter	2	37	0.087	1.361	0.269
Area×Perimeter	4	36	0.196	3.050	0.029*
B P/A ratio	1	37	0.008	0.125	0.725
Abundance					
Area	2	37	0.127	0.299	0.744
Perimeter	2	37	0.598	1.410	0.257
Area×Perimeter	4	37	0.958	2.257	0.081

binomial errors provided the best fit for models of functional group abundance (sessile, crawler, swimmer). The dataset included zero-count data that could not be normalized by transformation, resulting in overdispersion under a Poisson distribution. Consequently, we used generalized linear mixed models (GLMMs) for these analyses. Pairwise comparisons were calculated on least-squares means with the Tukey method for p-value adjustment.

We tested for the effect of subunit position (border vs. central) within transplants on community characteristics, with linear mixed effects models including the fixed variable position (2 levels: center or border position of subunit) as the main source of variation (Fig. 1). We also tested for the additional effect of core subunits on community characteristics, with the fixed variable core including 2 levels: with (core) or without borders along the transplant perimeter (Fig. 1). Replicate transplants were included as a random effect in the model (Table 2). Richness, total abundance [$\log_{10}(\text{density}+1)$] and Shannon diversity index, calculated for taxa and functional groups, were the dependent variables. We modified models described above to include the fixed variable position or core (Table 2). The same fixed and random structures described above were used in GLMMs with a binomial negative distribution for analysis on data of abundance (density) for each functional group (sessile, crawler, swimmer) as dependent variables.

Table 2. P-values extracted from linear mixed effects models with (A) the presence of a central subunit (2 levels) or (B) the position of the subunits (2 levels) within mussel transplants as a fixed variable. Transplant (36 levels) is included in models as a random variable. The dependent variables are the Shannon diversity index, taxonomic richness [$\log(\text{richness} + 1)$ transformed] and abundance [$\log(\text{density}) + 1$ transformed]. *Littorina* sp. was excluded from the dataset. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$, *** $p < 0.001$

Source of variation	Num df	Den df	Mean square	F	p
Shannon diversity index					
A Presence of a central subunit	1	34	1.981	13.071	0.001***
B Position of subunits	1	120	0.004	0.027	0.871
Taxonomic richness					
A Presence of a central subunit	1	36	0.858	7.007	0.012*
B Position of subunits	1	115	0.006	0.050	0.824
Abundance					
A Presence of a central subunit	1	36	0.459	0.082	0.305
B Position of subunits	1	110	0.034	0.080	0.777

We tested the effect of area (fixed with 3 levels), perimeter (fixed with 3 levels) and their interaction on species and functional group composition using permutational multivariate analyses of variance (9999 permutations; Anderson 2001). Transplant was included as a random effect (nested within the area \times perimeter interaction) and functional group abundances were fourth root transformed. We used the Gower Index to include double-zeros (Legendre & Legendre 2012). This index increases the similarity value between 2 transplants that include only a few taxa, and was used because potential overlap in species composition is expected to increase with species richness. *Littorina* sp. was not included in the data set (but see Table A1 in the Appendix). The sum of the fixed effects for mixed terms was zero and the sums of squares was of type III. It revealed no significant effect (Table A2 in the Appendix).

2.2.2. Ecosystem functions

We tested the effects of perimeter and area on ecosystem functions using the same linear mixed models described above. However, mussel mortality in transplants during the colonization period introduced variability in the density of live mussels, with potential effects on ecosystem processes. We thus first tested the effect of area (fixed with 2 levels), perime-

ter (fixed with 2 levels) and their interaction on oxygen uptake using analysis of covariance (ANCOVA) controlling for the number of live mussels at the time of incubation. This covariable showed a relationship ($p < 0.1$) with oxygen flux at 1 level of perimeter ($p = 0.081$, $R^2 = 0.422$ for the 160 cm perimeter group) and no relationship for other treatments or response variables. We thus conducted analyses of variance instead of ANCOVAs to test the effect of area and perimeter and the P/A ratio (fixed with 4 levels) on the rate of ammonium release.

3. RESULTS

3.1. Community of associated taxa

There was no effect of area and perimeter on *Littorina* sp. density (Table A1). Analyses conducted on the community data with (Table A1) and without *Littorina* sp. (Table 1) both revealed an effect of the perimeter–area interaction on taxonomic richness because *Littorina* sp. was present in all transplants and did not affect the mean richness of taxa. Excluding *Littorina* sp. also revealed an effect of the perimeter–area interaction on Shannon diversity index (Table 1). When the perimeter was small (160 cm), area had a negative effect on taxonomic diversity (richness, Shannon index, Fig. 2). Transplants with a small area also had a lower diversity (richness, Shannon index) at intermediate (180 cm) compared to small (160 cm) perimeter (Fig. 2).

The P/A ratio did not explain a significant part of the variation for any of our dependent variables (Table 1). The presence of a core subunit (without a border along the transplant perimeter) had a negative effect on whole-transplant taxonomic diversity (richness, Shannon diversity index; Table 2, Fig. 3). However, linear mixed models incorporating the fixed variable position revealed no difference in community characteristics between subunits with different positions in the transplant (Table 2).

3.1.1. Functional groups

We found that functional diversity (Shannon index) based on adult mobility was lower in transplants with a large area (Fig. 4, Table 3). We also observed a significant effect of the perimeter–area interaction on functional groups. There was a negative effect of area on functional group richness in small-perimeter transplants (Table 3, Fig. 5). Crawlers tended to be

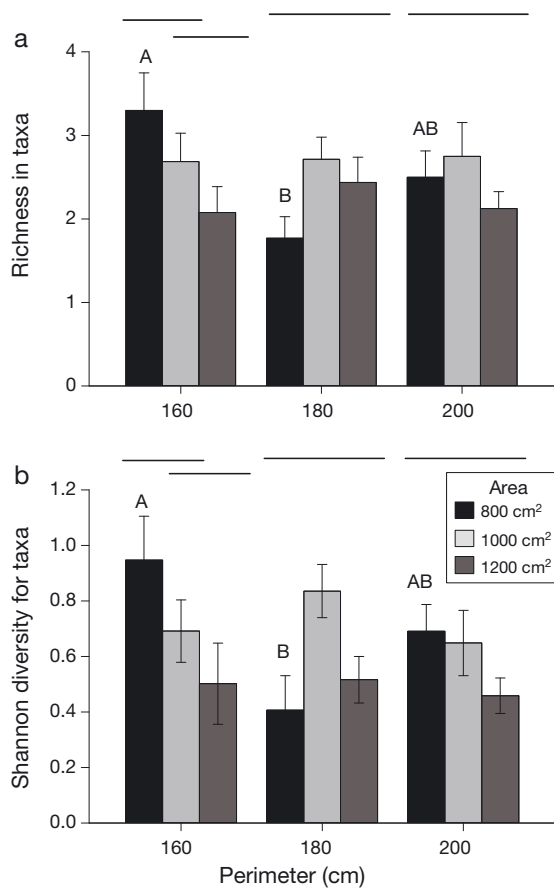


Fig. 2. Effects of transplant area and perimeter on (a) mean associated taxonomic richness, and (b) mean Shannon diversity index (\pm SE). Least-squares means (with Tukey method for adjustment of p-values for a family of 3 tests) were calculated for the factors 'area' and 'perimeter' of linear mixed effects models ($p < 0.05$). Horizontal black lines with different levels, above the bars, illustrate a significant difference within groups ($p < 0.05$). An unbroken line means no significant difference among adjacent bars. Different uppercase letters indicate significant differences between transplants of different perimeters for the same area size

less represented (Table A3 in the Appendix) in transplants of large area (1200 cm²) with a small perimeter (160 cm). Once again, the effect of the area–perimeter interaction was not explained by the P/A ratio (Table 3). Functional diversity and richness were lower in transplants with a core unit (Table 4, Fig. 6), and taxa with reduced adult mobility (sessile and crawler groups) were also less abundant in transplants with a core subunit (Table 5, Fig. 7).

3.2. Ecosystem functions

In contrast with community response observed mostly in small-perimeter transplants, increases in

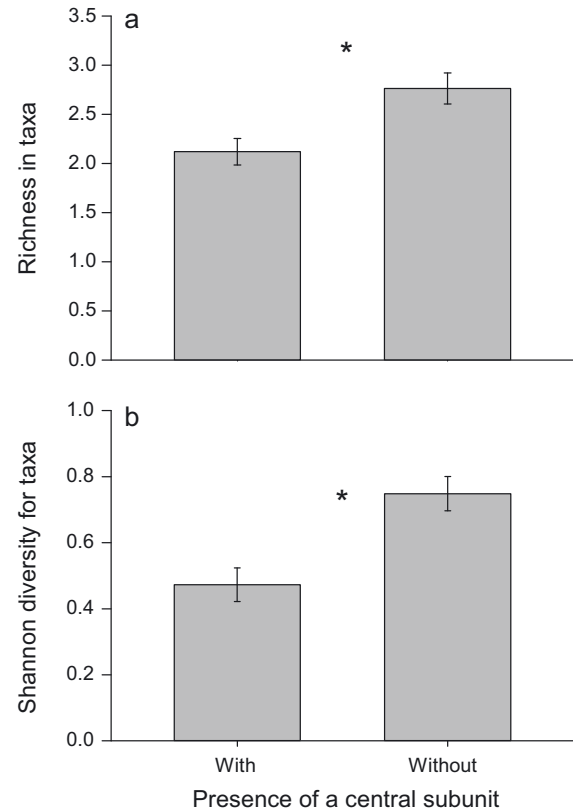


Fig. 3. Effects of the presence in the transplants of a central subunit on (a) mean associated taxonomic richness and (b) mean Shannon diversity index (\pm SE). A star above the bars indicates a significant difference between groups ($p < 0.05$)

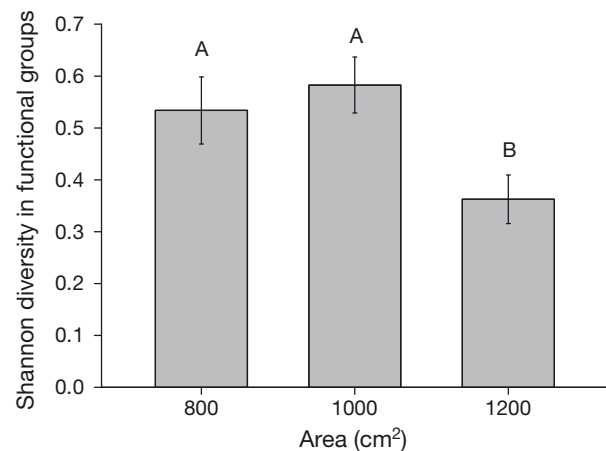


Fig. 4. Effects of the transplant area on mean Shannon diversity index (\pm SE) for functional groups. Different uppercase letters indicate significant differences between groups

ecosystem functions in response to patch geometry were observed in large-perimeter transplants. We found significant effects of area and perimeter on ecosystem processes (Tables 6 & 7). The oxygen uptake (% O₂ 20 l⁻¹ h⁻¹) by the community (mussels

Table 3. P-values extracted from linear mixed effects models testing (A) the effects of area and perimeter of mussel patches and (B) the effect of the perimeter to area (P/A) ratio on Shannon diversity index, richness in functional groups and abundance [log(density + 1) transformed]. The random effects of transplant were included in models. *Littorina* sp. was excluded from the data set. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$

Source of variation	Num df	Den df	Mean square	F	p
Shannon diversity index					
A Area	2	37	0.546	4.986	0.012*
Perimeter	2	38	0.084	0.770	0.470
Area×Perimeter	4	37	0.276	2.521	0.057
B P/A ratio	1	38	0.192	1.759	0.193
Richness in functional groups					
A Area	2	38	1.023	1.950	0.157
Perimeter	2	38	0.446	0.850	0.435
Area×Perimeter	4	37	1.400	2.664	0.047*
B P/A ratio	1	38	0.222	0.424	0.519
Abundance of functional groups					
A Area	2	37	0.127	0.299	0.744
Perimeter	2	37	0.598	1.409	0.257
Area×Perimeter	4	37	0.958	2.257	0.081

Table 4. P-values extracted from linear mixed effects models with (A) the presence of a central subunit (2 levels) or (B) the position of the subunits (2 levels) in mussel transplants as a fixed variable. Transplant (36 levels) is included in models as a random variable. The dependent variables are the richness, abundance [log(density + 1) transformed] and Shannon diversity index calculated for functional groups. *Littorina* sp. was excluded from the data set. A significance level of $\alpha = 0.05$ was used; ** $p < 0.01$, *** $p < 0.001$

Source of variation	Num df	Den df	Mean square	F	p
Shannon diversity index for functional groups					
A Presence of a central subunit	1	36	1.718	15.719	<0.001***
B Position of subunits	1	120	0.060	0.554	0.458
Richness in functional groups					
A Presence of a central subunit	1	36	4.687	8.930	0.005**
B Position of subunits	1	116	0.117	0.224	0.637
Abundance of functional groups					
A Presence of a central subunit	1	36	0.459	1.082	0.305
B Position of subunits	1	110	0.034	0.080	0.777

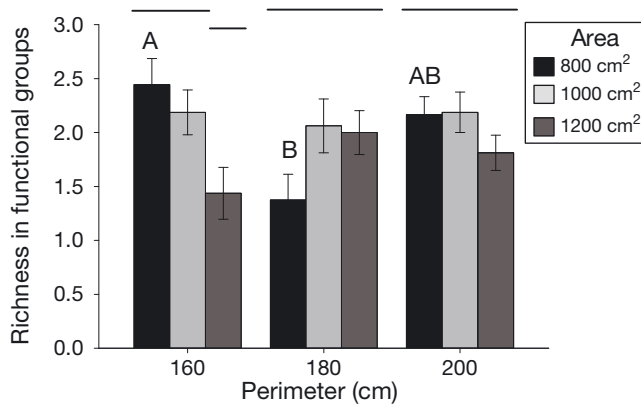


Fig. 5. Effects of transplant area and perimeter on mean richness (\pm SE) in functional groups. Least-squares means (with Tukey method for adjustment of p-values for a family of 3 tests) were calculated for the factors 'area' and 'perimeter' of linear mixed effects models ($p < 0.05$). Horizontal black lines with different levels, above the bars, illustrate a significant difference within groups ($p < 0.05$). An unbroken line means no significant difference among adjacent bars. Different uppercase letters indicate significant differences between transplants of different perimeters for the same area size

and associated taxa) was higher in large-perimeter transplants (Fig. 8). We also found a positive effect of area on ammonium release ($\mu\text{mol } 20 \text{ l}^{-1} \text{ h}^{-1}$) in large-perimeter transplants (Fig. 9). These effects of area and perimeter were again not revealed by the P/A ratio (Table 7).

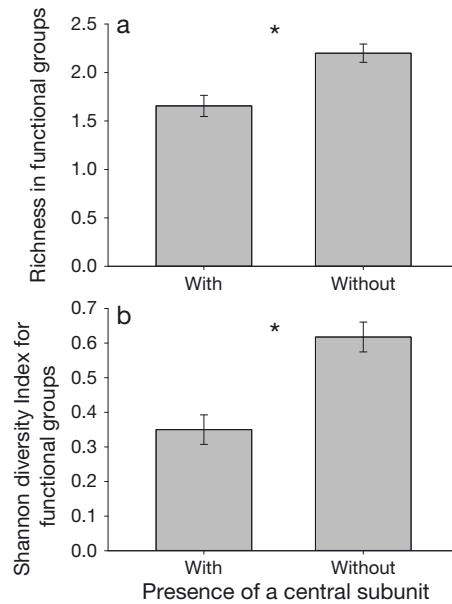


Fig. 6. Effects of the presence in the transplants of a central subunit on (a) mean richness in functional groups and (b) mean Shannon diversity index for functional groups (\pm SE). A star above the bars indicates a significant difference between groups ($p < 0.05$)

4. DISCUSSION

Several studies have examined the effect of mussel bed size on diversity of associated communities (Tsuchiya & Nishihira 1985, Koivisto & Westerbom 2012).

Table 5. P-values extracted from generalized linear mixed effects models with (A) the presence of a central subunit (2 levels) or (B) the position of the subunits (2 levels) in mussel transplants as a fixed variable. Transplant (36 levels) is included in models as a random variable. The dependent variables are the total abundance (density) for the functional groups 'sessile,' 'crawler' and 'swimmer.' *Littorina* sp. was excluded from the data set. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$

Source of variation	Num df	Den df	F	p
Abundance ('swimmer')				
A Presence of a central subunit	1	32	0.23	0.637
B Position of subunits	1	106	0.09	0.761
Abundance ('crawler')				
A Presence of a central subunit	1	42	5.39	0.025*
B Position of subunits	1	132	0.89	0.347
Abundance ('sessile')				
A Presence of a central subunit	1	32	4.44	0.043*
B Position of subunits	1	132	0.24	0.628

We controlled for perimeter and area of experimental mussel beds and tested their interacting effects on community structure and ecosystem functions. Our study revealed the non-additive effects of area and perimeter on the community of associated taxa, and on ecosystem functions in mussel beds. Our results further reveal the potential decoupling of ecosystem and community responses to landscape geometry: area had a negative effect on richness in small-perimeter transplants, whereas it had a positive effect on ammonium release in large-perimeter transplants. Our study suggests that the explicit treatment of multiple habitat shapes at both community and ecosystem levels can help understand the high variability in responses to habitat geometry across scales and systems, and to extend current theories linking commu-

nity structure and ecosystem functions to natural landscapes.

4.1. Multiple metrics of habitat geometry and of community response

Natural habitats have complex geometries that can be captured by many shape variables. However, ecology has developed a number of theories focusing on either single metrics (e.g. area) or on integrated descriptors of complex geometry, such as ratios of perimeter and area or distance from habitat edges (Airoldi 2003). Our study suggests the importance of identifying interactive effects of geometry variables to understand their non-additive effects.

4.1.1. Species–area relationship

The species–area relationship predicts an increase in the number of taxa with area (MacArthur & Wilson 1967, Root 1973, Gilpin & Diamond 1976). In contrast, we found a negative influence of mussel bed area on taxa richness when the perimeter was small (Table 1). The patch size effect is highly variable, and differences in taxa life history, functional traits and habitat can explain the divergence in response to area (e.g. Eggleston et al. 1998, Boström et al. 2011, Jones et al. 2015). Bender et al. (1998) found a negligible influence of area on generalists, a positive effect on taxa situated in the inner patch and a negative area effect on taxa located at the edge. Our results similarly showed the differential response of functional groups to habitat geometry, but also suggest the importance of resolving non-additive interactions between geo-

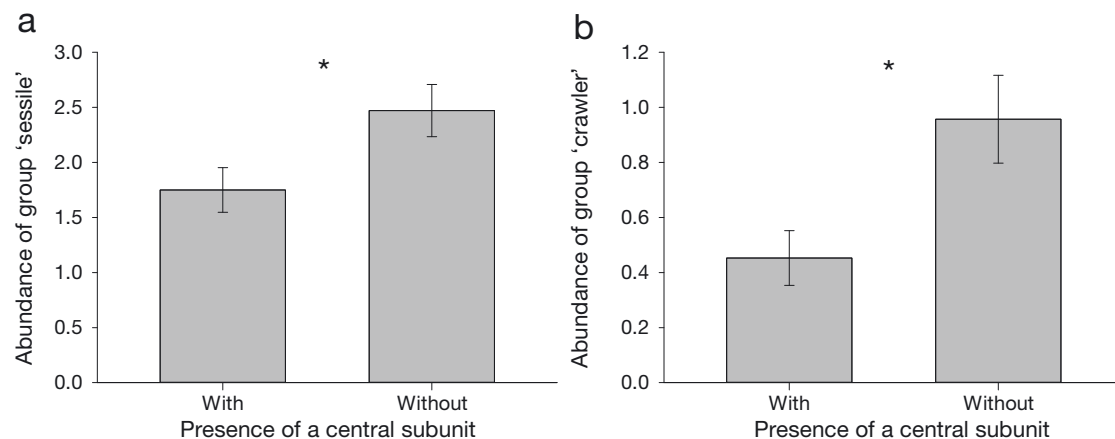


Fig. 7. Effects of the presence in transplants of a central subunit on mean abundance for the functional groups (a) 'sessile' and (b) 'crawler' (ind. transplant⁻¹ ± SE). A star above the bars indicates a significant difference between groups ($p < 0.05$)

Table 6. Results from ANCOVA testing the effect of area and perimeter of mussel beds on the rate of oxygen uptake, with the number of live mussels as a covariable. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$

Source of variation	df	Mean square	F	p
Number of mussels alive	1	1076.7	4.064	0.069
Area	1	3.8	0.014	0.907
Perimeter	1	1457.5	5.502	0.038*
Area×Perimeter	1	73.2	0.276	0.610
Residuals	11	264.9		

Table 7. Results from ANOVAs testing the effect of (A) area and perimeter of mussel beds on rate of ammonium release and (B) the effect of perimeter to area (P/A) ratio. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$

Source of variation	df	Mean square	F	p
A Area	1	343.1	4.325	0.060
Perimeter	1	29.2	0.368	0.555
Area×Perimeter	1	414.7	5.228	0.041*
Residuals	12	79.3		
B P/A ratio	1	239.0	2.231	0.157
Residuals	14	107.1		

metric properties of habitat in order to resolve the variation in species–area relationships.

4.1.2. Area–perimeter interactions

We showed that the effect of area on communities associated with mussel transplants was only observed

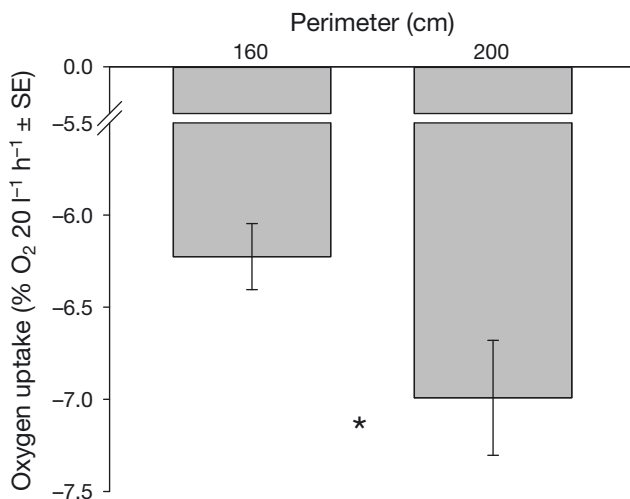


Fig. 8. Effects of the transplant perimeter on mean rate of oxygen uptake (\pm SE). A star between bars indicates a significant difference between groups ($p < 0.05$)

in small-perimeter transplants, thus revealing the non-additive effects of area and perimeter on communities. This result directly addresses the challenge of integrating multiple metrics of landscape complexity into indices that can be controlled in experiments and in the field. Sousa (1984, 1985) suggested that effects of habitat geometry in marine systems might be captured by the P/A ratio. A habitat of large area with a small perimeter, and consequently a small P/A ratio, is expected to present a higher diversity of environmental conditions that increases taxa richness (Helzer & Jelinski 1999, Arponen & Boström 2012). In contrast, we found that the P/A ratio did not significantly explain variability in community structure between experimental mussel transplants. The lowest species diversity was observed in transplants with the smallest P/A ratio (160 cm / 1200 cm²), and in transplants with complex shapes associated with a large P/A ratio (180 cm / 800 cm²).

Other mechanisms including the complexity of the perimeter line and edge effects (e.g. Botequilha Leitao & Ahern 2002, Ries et al. 2004, Nams 2014) could explain our results showing the loss of taxonomic diversity with increasing area in small-perimeter transplants. Edge effects can interact strongly with patch area (Jelbart et al. 2006). For example, an edge effect on fish richness in large seagrass habitats was observed by Jelbart et al. (2006) over some threshold patch area (>6500 m²), while area alone had a negative effect on taxa richness in small patches (7.2–13 m²).

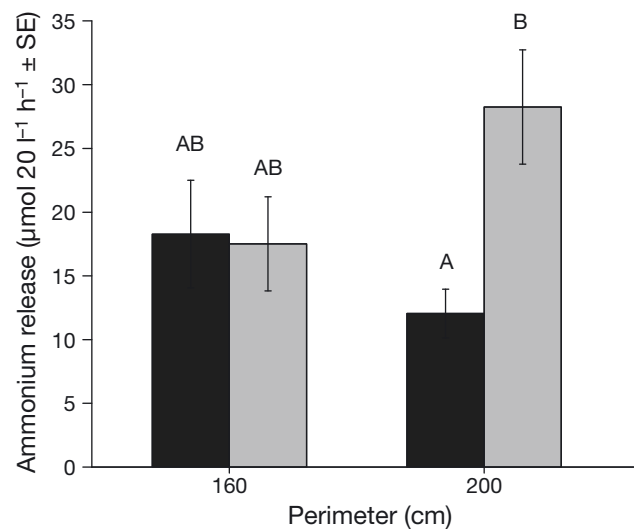


Fig. 9. Effects of transplant area and perimeter on mean rate of ammonium release (\pm SE). Black and light gray bars illustrate area values of 800 and 1200 cm², respectively. Different uppercase letters indicate significant differences between groups ($p < 0.05$)

4.1.3. Functional traits

The loss of taxonomic diversity with area in small-perimeter transplants was paralleled by the response of functional group diversity. Our mussel transplants were mostly colonized by low-mobility taxa, which is further compatible with the observed negative effect of area on functional group richness in small-perimeter transplants. This result illustrates the non-additive effect of habitat perimeter and area on community assembly. It could indicate that the importance of area for explaining edge effects on the colonization and recruitment of low-mobility species and on their access to resources can only be revealed under compact habitat geometries (small perimeter), rather than as a simple function of P/A ratios.

The accumulation of sediments, feces and pseudofeces in the center of mussel patches can create distinct environmental conditions between central and edge sections (Tsuchiya 1980). The lack of relationship between the P/A ratio and any of our measured response variables could suggest that the low structural complexity of sub-arctic mussel beds combined with the small spatial scale of our experimental transplants prevented the development of heterogeneity between their central and edge sections. However, the presence of a central subunit was related to community characteristics, with a lower average abundance of low-mobility taxa within the transplant in the presence of a central subunit. Because the effect of core subunits was detected at the scale of transplants (among-subunit variability), underlying mechanisms should be related to geometric properties of transplants with core subunits that are not captured by area and perimeter. Mechanisms could also have effects that propagate through the movement of individuals and sediments across transplants, and thus average over transplants with core subunits. High-mobility species have been shown to be less sensitive to patch area (Franzén et al. 2012). Our results suggested that they might be also less sensitive to other patch characteristics, as they were not significantly influenced by the presence of a central subunit.

4.2. Ecosystem functions

The study of relationships between community structure and ecosystem functions have contributed to the shift in emphasis from explaining species diversity to predicting its implications for the productivity and resilience of whole ecosystems (Loreau et al. 2002, Daufresne & Hedin 2005). These implica-

tions include ecosystem response to habitat loss and fragmentation. The role of community structure for mediating this response can be predicted by the correlation between response traits and effect traits, linking species response to ecosystem functions (Oliver et al. 2015). However, coupling of species-specific responses to habitat geometry to whole-ecosystem processes is still unresolved. We tested the effect of area, perimeter and their interaction on oxygen fluxes and ammonium release within mussel transplants. Results revealed a significant effect of the area–perimeter interaction on ammonium release (influencing nitrogen cycling), and of the perimeter on oxygen uptake, and suggest that invertebrate community and whole-ecosystem properties responded to different characteristics of habitat geometry.

Our experiment was designed to detect variations in ecosystem fluxes among transplant subunits that persisted when these were isolated from their experimental sites. These variations thus reflect time-integrated impacts of habitat geometry on the metabolism of the full ecosystem, including mussels, the associated invertebrate fauna and bacteria. Our results on community diversity similarly reflect a time-integrated effect of habitat geometry, but only on the colonization and survival of associated invertebrate species $>500 \mu\text{m}$. Our results suggest that landscape features affecting species colonization and persistence might not translate directly into whole-ecosystem functions. This is evidenced by the observed positive effect of area on ammonium release in large-perimeter transplants, while community-level variables responded to area in small-perimeter transplants.

Ammonium release from mussel beds is dominated by excretion from mussels (Largaespada et al. 2012) and is affected by the abundance of both the associated fauna and bacteria within the sediment layer (Christensen et al. 2003, Largaespada et al. 2012). Oxygen uptake, on the other hand, results from the metabolic activity of all ecosystem compartments, including mussels, the associated fauna and the microbial community. The fact that oxygen uptake increased with perimeter while ammonium release only increased with perimeter in large transplants suggests that over the scale of our study, the combination of large area and high perimeter benefited the metabolic activity of mussels, while large perimeter benefited the associated fauna and/or the accumulation of organic sediments and bacterial activity, leading to lower mussel metabolic activity measured as ammonium release. This would be compatible with the overall increase of oxygen uptake in large-

perimeter transplants, which would combine mussel uptake in large transplants, and uptake from other compartments in small transplants. This partitioning of ecosystem fluxes between compartments of the mussel beds could be compatible with the observed decrease in species diversity with transplant area. However, this community effect was only observed in small-perimeter transplants, which suggests the decoupled response of invertebrate colonization and of whole-ecosystem functions to habitat geometry. Perimeter could indirectly decrease ammonium release from mussels by mediating competition from other ecosystem compartments through fluxes and retention of organic matter and organisms (Ries et al. 2004).

Recent studies using experimental mussel transplants in intertidal systems also provided evidence for the importance of spatial structure for community and ecosystem dynamics in intertidal mussel beds but emphasized the role of among-patch connectivity (Largaespada et al. 2012). Our study provides evidence that patch geometry, in addition to connectivity, even over small spatial scales (800, 1000 and 1200 cm²), are important properties linking the response of community structure and ecosystem functions to habitat fragmentation. Our results suggest that linking community structure and ecosystem functions in natural landscapes depends on resolving the differential responses of community structure and ecosystem fluxes to habitat geometry, in addition to identifying response and effect traits at the species level (Oliver et al. 2015). They also strengthen the idea that studying interactions among multiple environmental drivers such as habitat area and perimeter will be key for improving the use of multiple functional traits to link community structure to ecosystem functions in disturbed environments (Mouillot et al. 2013).

4.3. Conclusion

Our results revealed non-additive effects of habitat area and perimeter on community and ecosystem properties. They highlight the importance of integrating the interacting effects of various metrics of spatial structure in the study of ecosystem response to habitat distribution. The independent manipulation of area and perimeter further revealed that the response of whole ecosystems to habitat geometry might be decoupled from the community-level response of the associated fauna. Further studies should resolve the mechanisms underlying such decoupling

in the response of ecosystems to landscape structure. Understanding the non-additive impacts of habitat geometry is relevant not only for the conservation and management of fragmented habitats, but also for applying current theories of community structure and ecosystem function to natural landscapes.

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Appendix. Additional model results

Table A1. Results from linear mixed effects models, with the fixed factors area (3 levels) perimeter (3 levels) and their interaction as the main sources of variation. The model included the random variable transplant (36 levels). The dependent variables are Shannon diversity index, taxonomic richness [log(richness + 1) transformed], abundance [log(density + 1) transformed] and abundance of *Littorina* sp. A significance level of $\alpha = 0.05$ was used; *p < 0.05

Source of variation	Num df	Den df	Mean square	F	p
Shannon diversity index					
Area	2	37	0.012	0.245	0.784
Perimeter	2	37	0.015	0.304	0.740
Area×Perimeter	4	37	0.104	2.144	0.095
Richness					
Area	2	37	0.081	1.269	0.293
Perimeter	2	37	0.087	1.360	0.269
Area×Perimeter	4	36	0.196	3.050	0.029*
Abundance of taxa					
Area	2	36	0.028	0.319	0.729
Perimeter	2	36	0.203	2.274	0.117
Area×Perimeter	4	36	0.058	0.648	0.632
Abundance of <i>Littorina</i> sp.					
Area	2	36.254	102.415	0.940	0.400
Perimeter	2	36.282	118.731	1.090	0.347
Area×Perimeter	4	36.243	93.705	0.860	0.49

Table A2. Permutational multivariate analysis of variance (9999 permutations) with Gower dissimilarity index on fourth root transformed data, testing the effect of area (fixed with 3 levels) and perimeter (fixed with 3 levels) on assemblies of taxa and functional groups, with transplant as random factor. Fixed effects sum to zero for mixed terms and sums of squares is of type III. *Littorina* sp. is not included in the data set. A significance level of $\alpha = 0.05$ was used; * $p < 0.05$, *** $p < 0.001$

Source of variation	df	Mean square	F	p
Taxa				
Area	2	24.72	0.696	0.674
Perimeter	2	26.43	0.746	0.639
Area×Perimeter	4	26.18	0.737	0.713
Transplant (Area×Perimeter)	27	35.97	1.479	0.004*
Residuals	90	24.32		
Functional groups				
Area	2	1311.50	1.053	0.414
Perimeter	2	339.24	0.273	0.829
Area×Perimeter	4	2098.90	1.676	0.153
Transplant (Area×Perimeter)	28	1284.50	2.827	<0.001***
Residuals	97	454.34		

Table A3. P-values extracted from generalized linear mixed effects models relating the fixed variables area and perimeter as well as the fixed variable perimeter to area (P/A) ratio, to abundance of the functional groups 'sessile', 'crawler' and 'swimmer'. Transplant is included as random variable in models. *Littorina* sp. is not included in the data set. A significance level of $\alpha = 0.05$ was used

Source of variation	Num df	Den df	F	p
Abundance ('swimmer')				
Area	2	25	1.11	0.900
Perimeter	2	25	0.53	0.595
Area×Perimeter	4	25	0.96	0.445
Abundance ('crawler')				
Area	2	37	0.81	0.452
Perimeter	2	38	0.82	0.449
Area×Perimeter	4	34	2.07	0.106
Abundance ('sessile')				
Area	2	23	1.45	0.254
Perimeter	2	24	2.35	0.117
Area×Perimeter	4	23	1.27	0.309