

Analysis of spatial niche structure in coexisting tidepool fishes: null models based on multi-scale experiments

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Summary

1. Fundamental and realized spatial niches were investigated through a combination of laboratory and mesocosm experiments, field observations and null model analysis in three intertidal gobiid species (*Bathygobius fuscus*, *Chaenogobius annularis* and *C. gulosus*). Null models based on the results of single-species experiments were used to assess interspecific spatial use and coexistence on two different scales: (i) microhabitats within a tidepool ('microhabitat' scale); and (ii) distribution among a set of tidepools ('habitat-wide' scale).
2. Patterns of microhabitat use varied from single to paired treatments, depending on paired species. Realized overlap of microhabitat use was smaller than would be expected from single-individual situations for intraspecific combinations, but not for interspecific ones.
3. Patterns of tidepool occupancy (a measure of spatial niche breadth) in the mesocosm were influenced by interspecific interactions. Two *Chaenogobius* species, but not *B. fuscus*, decreased tidepool occupancy in the hetero-specific treatments compared with the mono-specific ones. For all interspecific combinations, spatial overlap (habitat-wide scale) was significantly lower than the values expected from mono-specific situations. The results also indicated a possible trade-off between competitiveness and growth efficiency in these fishes.
4. Interspecific spatial overlap in the field was similar to that in the mesocosm experiment and the pattern of coexistence of gobiids can be explained by the results of our experiments.
5. This study demonstrates that niches of intertidal fishes may experience modifications under the influence of species interactions and that null models based on controlled experiments can greatly facilitate the deciphering of such changes in niche structure.

Key-words: coexistence, competition, intertidal, intra-/interspecific interactions

Introduction

The niche concept has been central to community ecology, on which major theoretical and empirical studies have been undertaken (e.g. Grinnell 1914; Elton 1927; Hutchinson 1957; MacArthur 1958; Pulliam 2000; Chase & Leibold 2003; Odling-Smee, Laland & Feldman 2003; Tilman 2004; McGill *et al.* 2006; Pearman *et al.* 2008; Levine & HilleRisLambers 2009). Species coexistence cannot be discussed fully without referring to the niche and the aspects of resource utilization (Hutchinson 1957; Schoener 1974), both of which have important implications for species assembly, species abundance and competitive/non-competitive relations (Tokeshi

1999). The shape and volume of niche may be altered through biotic interactions, most notably competitive relations on ecological and evolutionary time scales (Connell 1983; Schoener 1983; Morin 1999; Pearman *et al.* 2008). Conversely, the consequences of competitive interactions may be revealed through a comparison between the fundamental and the realized niche, which would lead to a better understanding of the mechanics of community organization and species coexistence.

Space is an important dimension of niche which may be shared or partitioned by co-occurring species (Schoener 1974; Tokeshi 1999), reinforcing the view that resource partitioning in terms of space is central to species coexistence (e.g. Rosenzweig 1981). Fundamental spatial niche depends on the ecophysiological and other traits of a species, forming the basis of species-specific occurrence patterns which in turn are closely influenced by requirements for food, reproduction, avoidance of predators/competitors and some adverse

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environmental conditions. The distribution of species and, consequently, species composition and coexistence in a community reflect some modifications of the fundamental spatial niches of different species. Possible effects of competition on habitat use (i.e. changes in spatial niche), in particular, have often been inferred through experimental manipulations of competitor abundance in various assemblages (e.g. Crowell & Pimm 1976; Black 1979; Hairston 1980; Pacala & Roughgarden 1982; Elmberg *et al.* 1997; Lee & Silliman 2006) including fishes (e.g. Werner & Hall 1976, 1977; Munday, Jones & Caley 2001; Schofield 2003). However, assessment of changes in spatial niche is not straightforward with experiments, as biological realism may be sacrificed and density and species identity cannot always be independently controlled in mixed-species situations. In this respect, incorporation of null model approaches may be of some value, but there has been no attempt to explore the possibility of combining manipulative experiments with null model analyses to elucidate patterns of niche shifts.

Despite numerous ecological studies on intertidal fishes, mechanisms and relative importance of different types of biotic interactions in community organization still remain obscure (see Gibson & Yoshiyama 1999). As the number of tidepools available at low tide time is limited, space is probably the most important niche dimension for intertidal fishes. Indeed, previous studies noted differences in spatial use (e.g. Gibson 1972; Davis 2000) and the possible roles of intra-/interspecific competition for space in structuring intertidal fish communities (e.g. Stephens *et al.* 1970; Nakamura 1976; Mayr & Berger 1992; Pfister 1995, 2006; Faria & Almada 2001). There is, however, a paucity of information on variable patterns of intra- and interspecific space use on different scales of intertidal habitat.

The objective of this work was to investigate the patterns of fundamental and realized spatial niche in intertidal gobiid species through a combination of laboratory and mesocosm experiments and null model analysis. Here, fundamental spatial niche was interpreted as spatial patterns shown by individuals of a species, either singly or as group of individuals. Null models were constructed from data derived from single-species/individual experiments in which there was no influence of inter-/intraspecific interactions. Spatial niche was considered on two different scales (microhabitat and habitat-wide) to examine the varied influences of biotic interactions on the patterns of space utilization and species coexistence in this assemblage. In assessing the influences of biotic interactions, growth was also taken into account alongside changes in space use.

Materials and methods

STUDY SITE AND FISH SPECIES

Field observation and fish collection were carried out on a moderately wave-exposed rocky shore of Shikizaki (32°31'N, 130°01'E) on the Amakusa-Shimoshima Island, south-western Japan. The study site had a tidal amplitude of about 3.5 m and was exposed for a

distance of about 80 m seaward at the low tide. Tidepools of various sizes formed on this relatively flat rocky shore. The observation area and the collection site were separated by > 100 m and an extra large tidepool (c. 3×10^4 m²) in between. Thus, there was no or negligible effect of fish collection on the observation area.

Gobiidae and Blenniidae were particularly abundant in the study site, with the former being dominant at all tidal levels, especially in the upper intertidal, constituting about 90% of tidepool fish community (Arakaki & Tokeshi 2006). Three common gobiid species chosen for the present study, *Bathygobius fuscus* (Rüppell), *Chaenogobius annularis* Gill and *Chaenogobius gulosus* (Sauvage), comprised over 80% of tidepool fish fauna throughout the year. All three species are adapted for benthic life with similar maximum body sizes (c. 10 cm total length), compressed body shape and cryptic coloration, and are known to consume small benthic animals (Dôtu 1955; Sasaki & Hattori 1969).

Field observations on tidepool use were conducted in the same season as the mesocosm experiment (June–August 2003, see below). A total of 34 tidepools of various sizes (surface area 500–9500 cm²) were chosen from the mid to upper intertidal zones [170–255 cm above mean lower low water (MLLW)]. Species and their abundances were recorded by direct visual observation at day-time new moon spring low tide. We confirmed that this method had a similar accuracy of sampling as fish collection using anaesthetics (Arakaki & Tokeshi 2006).

LABORATORY EXPERIMENT ON MICROHABITAT USE

A laboratory experiment was carried out to examine the patterns of microhabitat utilization under the influence of biotic interactions. The present experiment with paired individuals complemented our previous experiment (Arakaki & Tokeshi 2005) that dealt solely with single-individual situations; results from both were used in the present study. Individuals of three species used in the experiment were collected using a hand net from the collection site. Fishes were carefully brought back to the laboratory in a container within 10 min of collection. All individuals were identified to species but sexes were not separated, as *Chaenogobius* spp. could not be sexed on the basis of external morphology. Fishes were selected for similar body sizes (mean TL \pm 1SD, *B. fuscus* = 38.5 \pm 4.2 mm, *C. annularis* = 36.1 \pm 2.2 mm and *C. gulosus* = 39.4 \pm 2.6 mm). Each species was kept separately in aquaria (62 \times 38 \times 15 cm) containing a bed of small stones with a flow-through seawater system for 7 days prior to the experiment. The fish were fed daily with pieces of shrimps, crabs and molluscs collected from the field. The acclimatization period of 7 days was considered appropriate for these gobiid fishes, though shorter than in other studies (Mayr & Berger 1992; Griffiths 2002; Schofield 2003).

The experiments were conducted in rectangular opaque aquaria (37 \times 25 \times 14 cm, corresponding in size to small natural tidepools), each of which was subdivided into four equal quarters by thin retention walls (2 cm high, 0.8 mm thick) and a square stone plate (10 \times 10 \times 1 cm) was placed in the centre to serve as a rooftop such that a fish could use the shaded space below as shelter (Fig. 1a). Each quarter of an aquarium was allotted with one of four types of substrate, (i) sand (diameter, 0.25–1.0 mm); (ii) coarse sand (1.0–5.6 mm); (iii) gravel (5.6–19 mm); and (iv) bare rock (stone tile); the positioning of the four substrates in an aquarium was determined randomly for each setup. Substrates were collected from the field and separated using sieves of different mesh sizes in the laboratory. Stone tiles used as bare rock were preconditioned in the field for a year prior

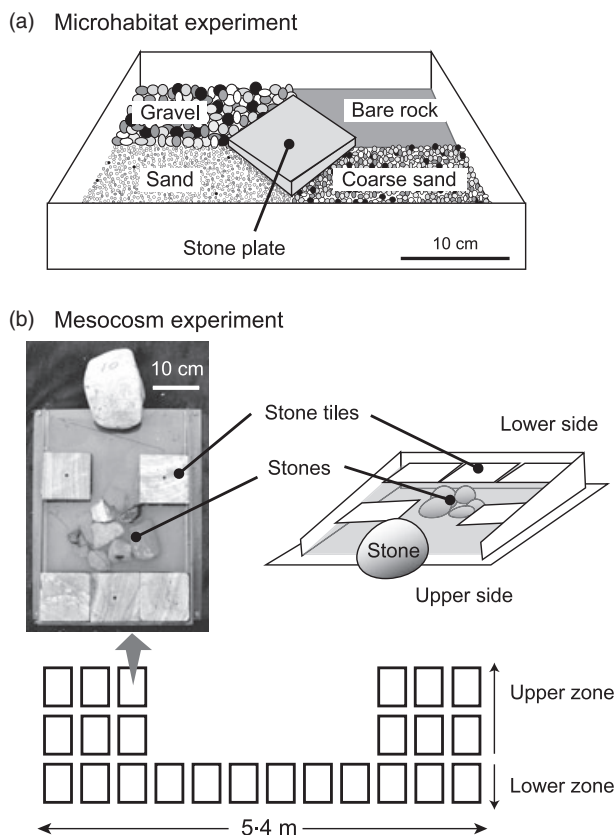


Fig. 1. Experimental setup of (a) the microhabitat experiment and (b) the mesocosm experiment. (a) shows an aquarium with a stone plate in the centre as shelter for fishes and different substrates in four areas. (b) shows details of an artificial tidepool with tilted sides and the arrangement of 24 of these in the mesocosm arena.

to the experiment. All sessile organisms attached were scraped off and all substrates were dried under the sun for 2 days before the experiment. The aquaria with substrates were conditioned with running seawater before each experimental trial.

Six combinations (three intraspecific and three interspecific) were investigated in the laboratory experiment. Prior to experiment, fishes were chosen arbitrarily from the maintenance aquaria and introduced into the centre of an experimental aquarium 6 h before the actual observation. This imitated the situation where a fish moved into a new tidepool before low tide under natural tidal cycles. Eight pairs of each interspecific combination were introduced into separate aquaria (i.e. two fish per aquarium) to serve as replicates, while there were four pairs for each intraspecific combination. Water depth was kept at 5 cm to imitate natural tidepool conditions at low tide; a fish could move freely between substrates. Aquaria were covered with a transparent plate to prevent gobies from escaping.

A 1-h observation was carried out for each pair of fish during which positions in the aquarium (a total of 10 categories: four substrates \times outside/inside the shelter, on top of the shelter, on the side wall) were recorded at 2-min intervals during day-time (between 13:00 and 15:00 hours) or night-time (21:30–23:30 hours). Thus for each individual, a total of 30 position data were obtained. A hand torch covered by a red film was used for night-time observations. It was turned off during the intervals of checking fish positions to minimize disturbance; fish apparently behaved normally (i.e. no sign of escape/stress responses such as quick changes in movement) throughout an observation session. Fishes were recognized

individually by species, relative body size and the peculiarities of their colour patterns. When a fish changed its location at the time of observation, only the first position was recorded. If a fish was on a boundary of zones, its location was determined according to where the majority of body mass existed and/or the position of its head. After each observation individuals were returned to maintenance aquaria; all fishes were released to the field on completion of the experiments.

MESOCOSM EXPERIMENT ON HABITAT-WIDE SPATIAL USE

A medium-scale artificial tidepool (mesocosm) experiment was conducted to investigate habitat-wide space utilization. The mesocosm was established on a semi-natural intertidal shore 1.5 km from the field site that was protected from wave exposure by concrete wall but had natural tidal fluctuations. An area of 6.3 \times 5.4 m was enclosed by a net (5 mm mesh) of 1.7 m high and the bottom was cleared of large stones and covered by thin wood panels to create a uniform substrate with a natural slope. In the enclosure, artificial tidepools (46 \times 30 \times 7 cm) were arranged in two different tidal zones: 12 tidepools in the upper zone in two rows (205–219 cm above MLLW) and 12 in the lower in one row (192–196 cm MLLW) separated by 15 cm gaps (Fig. 1b). Each artificial tidepool had a dustpan-like shape with sloping sidewalls such that, when placed on a sloping mesocosm floor, the upper, open side was flush with the mesocosm floor so that fish could enter the pool without hindrance as the tide receded. One stone was placed at the upper entrance to serve as a landmark for fishes and stone tiles and stones were placed inside as microhabitats (Fig. 1b).

Three gobiid species with similar size ranges as in the microhabitat experiment (mean \pm 1SD: *B. fuscus* = 38.7 \pm 3.0 mm, *C. annularis* = 37.1 \pm 1.5 mm, *C. gulosus* = 39.1 \pm 3.2 mm) were used in this mesocosm experiment. Body sizes of fishes were measured, after anaesthetizing, to the nearest 0.01 mm (TL) using digital callipers before and after introduction into the experimental arena. Fish individuals were marked by injecting visible implant fluorescent elastomer tags (Northwest Marine Technology, Shaw Island, Washington, USA) 1 week before the experiment. The tag was considered suitable for small fishes as it was known to have high retention (Griffiths 2002). Six different treatments [three mono-specific and three hetero-specific (two-species) combinations] were run as separate trials with a total of 48 individuals each (either 48 individuals of the same species or 24 individuals each of two species; two individuals per tidepool). In the case of interspecific combinations, different species were paired in each artificial tidepool at the time of introduction. Fishes could swim about freely and feed on small organisms in the mesocosm at high tide and retreat into artificial tidepools at low tide. Identity and the number of individuals in each artificial tidepool were recorded at consecutive low tides for a week after introduction. Individual that failed to use an artificial tidepool were collected and kept in the maintenance aquarium during low tide and released again into the mesocosm at the next rising tide. Few individuals that went missing during an experiment were not replaced. All fishes were released to the collection site after the experiments.

DATA ANALYSIS

Null model analysis

Null models were employed to evaluate the effects of biotic interactions. A single most crucial element of null modelling concerns

the creation of 'null expectation', a pattern in which a focal biological phenomenon is absent. In the case of biotic interactions, the situation without such interactions cannot in principle be re-created from observed data as there is generally no guarantee that the aspect of relevance extracted from the data concerned has not been influenced by those interactions, past and present. In the present study our rationale was to construct null models based on experimental manipulations in which a single species/individual was present, thereby guaranteeing that the expected patterns were devoid of biotic interactions. For the microhabitat (laboratory) experiment, the null model involved randomization based on two single-individual experimental results to create null expectation of (pairwise) space use. For the habitat-wide (mesocosm) experiment, the null model was generated by randomly combining two single-species (not individual) experimental results. The choice of individual-based or species-based procedures was related to the fact that individual-based situations become less realistic as spatial scale increases; while a single-individual situation is relevant at microhabitat or 'within-pool' scale, it is not at habitat-wide or 'among-pool' scale. Note that these two analyses for different spatial scales involved different details of null model construction, as explained below.

Microhabitat overlap (laboratory experiment)

Overlap (M_{β}) in microhabitat use was calculated as,

$$M_{\beta} = \sum_i \min(P_{x(i)}, P_{y(i)})$$

where $P_{x(i)}$ and $P_{y(i)}$ are the proportional use of the i th (micro-) habitat by species/individual x and y , respectively. Proportional use was based on the 30 position data for each individual from the laboratory experiment. The index ranged from 0 (no overlap) to 1 (complete overlap) (Tokeshi 1986, 1999). Realized (observed) overlap values were compared with expected values derived from the data of single-individual experiment (conducted under the same setup, Arakaki & Tokeshi 2005), assuming that paired fishes behave in the same manner as in a single-individual situation (i.e. not influenced by other individuals). To generate the expected pattern, a computer simulation was performed in which fishes were re-distributed among ten microhabitats according to the probabilities equalling the observed proportions of microhabitats occupied in the single-individual experiment (Table 1). This re-distribution process was repeated 30 times for each fish individual to generate a set of space-use (30 positions) data, which was then used to calculate spatial overlap for a particular pair of individuals. The whole procedure was replicated 1000 times with random selection of individuals to obtain the mean with 95% range for each intra-/interspecific combination.

Tidepool occupancy and overlap (mesocosm experiment)

Tidepool occupancy, expressed as the proportion of tidepools occupied out of total, represents a measure of spatial niche breadth on the mesocosm scale. Realized tidepool occupancy and overlap in tidepool use under hetero-specific mixtures were compared with the expected occupancy/overlap values based on the mono-specific treatment in the mesocosm experiment. To derive expected values, the following procedure was taken: (1) data on 24 individuals of each species were randomly extracted from the mono-specific treatment (a total of 39 *B. fuscus*, 43 *C. annularis* and 45 *C. gulosus*) individuals, excluding those with incomplete spatial data), (2) for each pair of species (a total of 48 individuals), tidepool occupancy was calculated for (i) each species separately and (ii) the two species together ('combined' occupancy; note that this value is equal to or smaller than the smaller of 1.0 and the addition of two separate occupancy values, depending on the degree of overlap in spatial distribution between the two species), (3) for each pair of species, spatial overlap (M_{β}) was calculated, using each tidepool as unit of habitat. In addition, 'observed' values of intraspecific overlap in tidepool use were obtained by randomly dividing the observed mono-specific set of 48 individuals into two groups (each with 24 individuals) and calculating the spatial overlap between the two groups. These procedures were repeated 1000 times to obtain the mean and 95% range of occupancy and overlap values. Although data were collected on 10–14 consecutive occasions (designated as $t1$ to $t10/t14$), only those of the last three occasions ($t8-t10$ or $t12-t14$) were subjected to this analysis, as these represented more reliable 'settled' patterns.

Interspecific spatial overlap was also calculated for field-derived data, separately for each species combinations on monthly occasions.

Change in tidepool use (mesocosm experiment)

Effect sizes were calculated for three aspects of habitat-wide space utilization in the mesocosm experiment: (i) number of 'displaced' individuals (i.e. those located outside the 24 aquaria in the mesocosm), (ii) upper/lower positioning (the ratio of individuals located in the upper and lower tidepools) and (iii) level of aggregation, expressed as Morisita's index (I_{δ}). In meta-analyses, the 'effect size' (D) is calculated by standardizing the difference between 'control' and 'experimental' groups (Gurevitch *et al.* 1992; Gurevitch & Hedges 2001). In our analysis, the mean values in the hetero-specific treatment (X_e) and that in the mono-specific treatment (X_c) correspond to the 'experimental' and the 'control' group, respectively. Thus, positive/negative values of D imply departures of the hetero-specific situations from the mono-specific ones. We calculated the effect size D using the pooled standard deviation (S) of the mono-specific and the hetero-specific treatments:

Table 1. Frequencies of microhabitat use (% , inside/outside shelter) by three gobiid species, under single-individual conditions

		Microhabitat category					
		Sand	Coarse sand	Gravel	Bare rock	Above plate	Side wall
<i>B. fuscus</i>	Day	6.7/30	1.7/17.9	12.1/23.8	0.8/2.1	1.7	3.3
	Night	2.5/23.3	2.5/14.2	3.3/42.9	2.1/7.9	1.3	0
<i>C. annularis</i>	Day	24.6/12.1	14.6/6.3	15/8.8	9.2/3.8	0.4	5.4
	Night	5.8/12.1	5.8/7.9	15.4/21.7	2.9/5	2.9	20.4
<i>C. gulosus</i>	Day	0/0	45.4/0.4	50/0	4.2/0	0	0
	Night	42.5/5.4	0/2.5	29.6/5.4	12.9/0.4	0.4	0.8

$$D = \frac{X_e - X_c}{S} J$$

$$S = \sqrt{\frac{(N_e - 1)S_e^2 + (N_c - 1)S_c^2}{N_e + N_c - 2}}$$

where S_e , S_c , N_e and N_c are the standard deviation (S) and the number of cases (N) of the hetero-specific treatment (e) and the mono-specific treatment (c), respectively. The term J corrects for bias due to small sample size:

$$J = 1 - \frac{3}{4(N_e + N_c - 2) - 1}$$

Growth in the mesocosm experiment

Growth rates, expressed as $(TL_2 - TL_1)/TL_1$ (where TL_1 and TL_2 are length at the start and the end of experiment, respectively), were compared between the mono-specific and the hetero-specific treatment using the Kruskal–Wallis test with Scheffe's *post hoc* test. For *B. fuscus*, the Mann–Whitney U -test was used to compare the mono-specific treatment (sample size was reduced to 37 due to missing values) and the mixture with *C. annularis*; the data on *B. fuscus* + *C. gulosus* combination were incomplete due to typhoon interruption. There were no significant differences in the initial mean size of introduced fishes among all treatment groups (ANOVA, $P > 0.05$).

Standardized mean differences of growth rates between the hetero-specific and the mono-specific treatment were also calculated in the same way as mentioned above (change in tidepool use). In this analysis, mean growth in the hetero-specific treatment (X_e) and that in the mono-specific treatment (X_c) correspond to the 'experimental' and the 'control' group, respectively.

Results

MICROHABITAT USE AND OVERLAP (LABORATORY EXPERIMENT)

On the microhabitat scale, the patterns of substrate use under mixed situations departed significantly from those expected under single situations for all combinations and times of day (chi-squared test with Bonferroni correction, $P < 0.05$) (Table 2). In contrast, the patterns of shelter use showed no such difference (Mann–Whitney U -test with Bonferroni correction, corresponding to $P > 0.05$) except for the *C. annularis* + *C. gulosus* pair by daytime. Realized values of intraspecific overlap in microhabitat use were significantly lower than would be expected from single situations in two *Chaenogobius* species and marginally so in *B. fuscus* (Fig. 2). In contrast, realized values of interspecific overlap showed no significant departure from expected values, except the *C. annularis* + *C. gulosus* pair by daytime. *Ca* + *Cg* was the only combination showing a clear difference in overlap pattern between day and night.

TIDEPOOL OCCUPANCY AND OVERLAP (MESOCOSM EXPERIMENT)

Tidepool occupancy of *B. fuscus* under interspecific mixtures showed no significant departure from the mono-specific

Table 2. Comparison of microhabitat use between single and mixed treatments of tidepool fishes. Changes in microhabitat use when mixed with other conspecific/heterospecific individual are tested for each focal species by the chi-squared test for substrate use and the Mann–Whitney U -test for shelter use. * $P < 0.05$ with Bonferroni correction

		Mixed species					
		+ <i>B. fuscus</i>		+ <i>C. annularis</i>		+ <i>C. gulosus</i>	
Focal species		χ^2	U	χ^2	U	χ^2	U
<i>B. fuscus</i>	Day	39.1*	22	26.1*	32	77.7*	29.5
	Night	75.6*	21	26.3*	15	68.7*	18.5
<i>C. annularis</i>	Day	30.1*	8.5	50.2*	14.5	117*	0*
	Night	81.7*	30.5	44.9*	28.5	103*	23.5
<i>C. gulosus</i>	Day	54.8*	13.5	95.2*	31.5	52.1*	19
	Night	122*	15.5	1499*	23	1958.5*	28.5

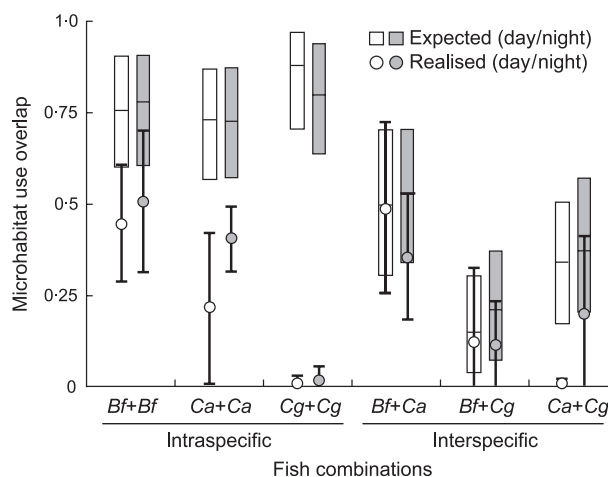


Fig. 2. Expected (bars, mean with 95% range) and realized (circles, mean \pm 1SD) overlap in microhabitat use for different combinations of fish. *Bf*, *Bathygobius fuscus*; *Ca*, *Chaenogobius annularis*; *Cg*, *C. gulosus*.

situation, while *C. annularis* and *C. gulosus* showed some significant departures (Fig. 3). *Chaenogobius annularis* had a significant reduction in tidepool occupancy when mixed with either *B. fuscus* or *C. gulosus*. Realized occupancy of *C. gulosus* varied depending on paired species: it was smaller when mixed with *C. annularis* but tended to be similar/slightly larger when mixed with *B. fuscus* than would be expected under mono-specific situations. Realized total (combined) occupancy of the *B. fuscus* + *C. gulosus* pair was larger than the expected value, while values for *B. fuscus* + *C. annularis* and *C. annularis* + *C. gulosus* pairs were smaller.

In all hetero-specific treatments, realized overlap values in the mesocosm were significantly smaller than would be expected from the mono-specific treatments and similar to observed values in the field (Fig. 4). The observed values of overlap in the field were apparently small compared with expected values of the mesocosm except for the June data of

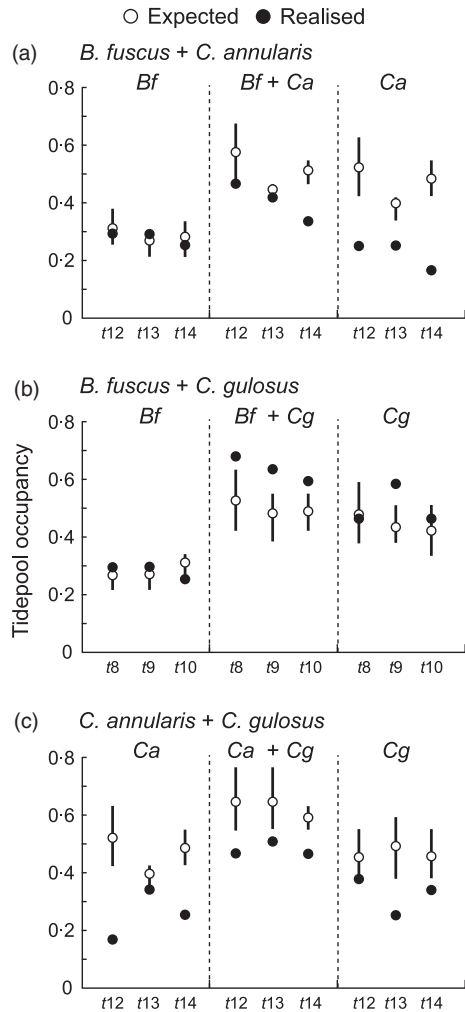


Fig. 3. Expected (open circles, mean with 95% range) and realized (filled circles) values of tidepool occupancy under three different hetero-specific treatments (a), (b) and (c) of the mesocosm experiment. Left and right panels of each figure show tidepool occupancy of each species and the middle panel shows total (combined) occupancy of two species, under the designated hetero-specific treatment. Last three observations of each treatment (designated as t_{12} – t_{14} , t_8 – t_{10}) are shown.

B. fuscus + *C. gulosus* combination. Observed intraspecific spatial overlap had similar magnitudes in the three species, being slightly shifted towards larger values than the expected interspecific overlap of *B. fuscus* + *C. annularis* and *B. fuscus* + *C. gulosus* pairs.

CHANGE IN TIDEPOOL USE (MESOCOSM EXPERIMENT)

Three gobiid species showed contrasting patterns of tidepool use under the hetero-specific treatment compared with the mono-specific one (Fig. 5). *Chaenogobius gulosus* paired with *C. annularis* showed a significant increase in the number of displaced individuals, while other species and species combinations showed no change (Fig. 5a). Two *Chaenogobius* species significantly changed their upper/lower positioning depending on paired species, while *B. fuscus* did not

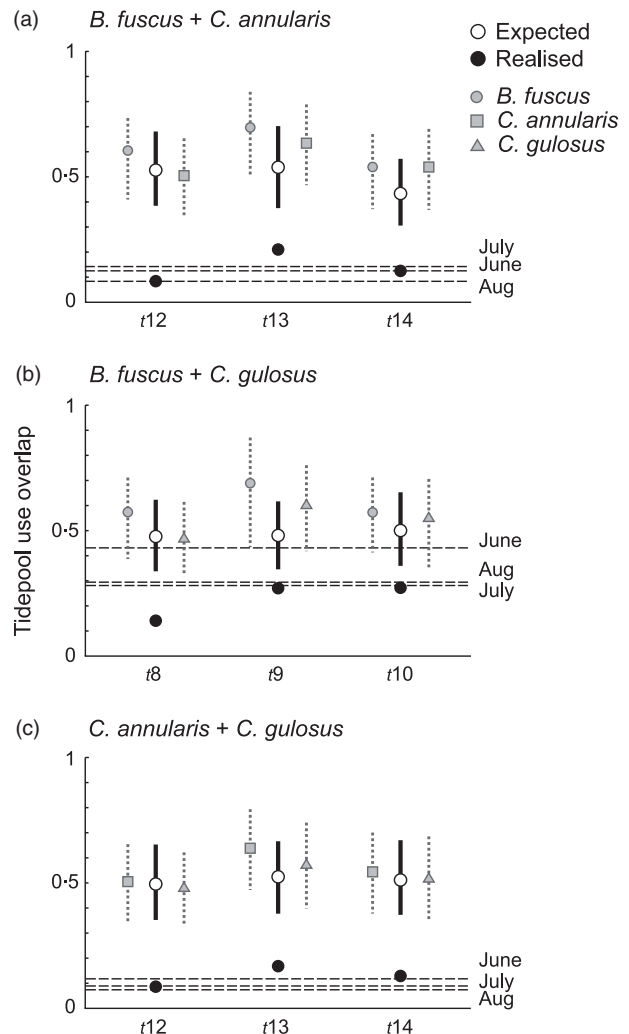


Fig. 4. Inter- and intraspecific overlap in tidepool use in the mesocosm experiment. Expected (open circles, mean with 95% range) and realized (filled circles) interspecific overlap of each hetero-specific treatment are shown, alongside calculated intraspecific overlap (half-tone symbols with dotted lines, mean with 95% range). Last three observations of each treatment (designated as t_{12} – t_{14} , t_8 – t_{10}) are shown. Dotted horizontal lines indicate field-observed interspecific overlap in June, July and August.

(Fig. 5b). *Chaenogobius annularis* tended to shift towards the lower intertidal when mixed with other species, particularly *C. gulosus*. In contrast, *C. gulosus* moved towards the upper intertidal when mixed with *B. fuscus*, but towards the lower intertidal when mixed with *C. annularis*. The degree of aggregation significantly increased in *C. annularis* but not in other species (Fig. 5c).

GROWTH IN THE MESOCOSM

Chaenogobius annularis showed significantly reduced growth rates in hetero-specific treatments compared with the mono-specific treatment (Fig. 6a Kruskal–Wallis test with Scheffé's *post hoc* test, $P < 0.05$). *Bathygobius fuscus* showed a similar trend, with a reduced growth rate in the mixture with *C. annularis* (Mann–Whitney *U*-test, $P < 0.05$) compared

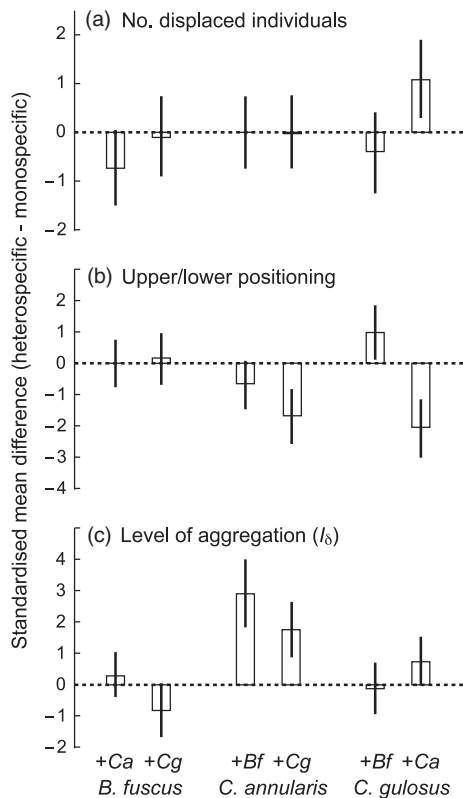


Fig. 5. Discrepancy in habitat utilization between the mono-specific and the hetero-specific treatment in the mesocosm experiment. Standardized mean difference (open bars with 95% CLs) in (a) the number of 'displaced' individuals (those located outside the 24 artificial tidepools), (b) upper/lower positioning (ratio of individuals in the upper and lower tidepools), (c) level of aggregation (Morisita's I_s).

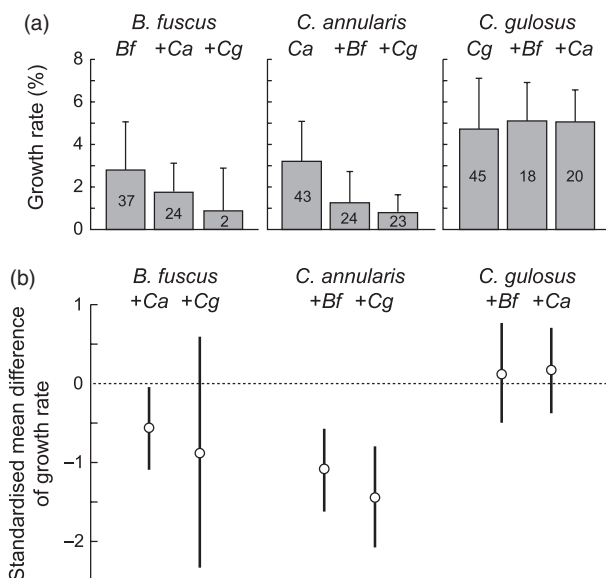


Fig. 6. (a) Growth rates (mean \pm 1SD) under different intra-/interspecific combinations of the mesocosm experiment. Numbers on each bar indicate sample size. (b) Standardized mean difference of growth rates (\pm 95% CLs) between mono-specific and hetero-specific treatment.

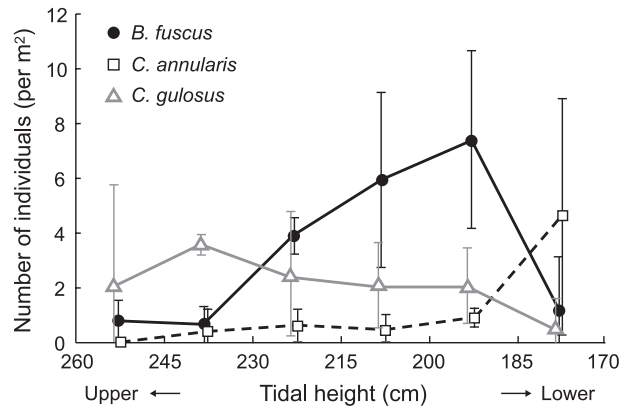


Fig. 7. Variation in density (number per unit surface area of tidepools, mean \pm 1SD) of fish in relation to the vertical position of tidepools (classified into six height levels).

with the mono-specific treatment; the *B. fuscus* + *C. gulosus* combination was similar to *Bf* + *Ca*, though its small sample size did not allow a definite comparison. In contrast, no significant difference in growth rates between treatments was detected for *C. gulosus*. These trends were also demonstrated by the standardized mean difference of growth rates (Fig. 6b), with *B. fuscus* and *C. annularis* (but not *C. gulosus*) experiencing a negative effect from the presence of other species.

DISTRIBUTION IN THE FIELD

Three gobiid species showed distinct patterns of vertical distribution, with peak densities consistently found at different tidal levels (Fig. 7). *Chaenogobius gulosus* was more evenly distributed from the mid intertidal upwards with relatively higher abundances in the upper intertidal, *B. fuscus* was most abundant in the mid-low intertidal and *C. annularis* was concentrated in the lowest zone.

Discussion

ANALYSIS OF FUNDAMENTAL VS. REALIZED SPATIAL NICHE

A combination of habitat-use experiments on different spatial scales and null model analyses allowed the evaluation of intra- and interspecific interactions in the spatial utilization and community organization of intertidal fishes. In previous studies the effect of species interactions on community structure has been examined through either experimental (e.g. Black 1979; Pacala & Roughgarden 1982; Elmerg *et al.* 1997; Munday, Jones & Caley 2001; Schofield 2003) or analytical approaches (e.g. Sale 1974; Lawlor 1980; Tokeshi 1986; Winemiller & Pianka 1990; Tokeshi & Romero 2000; Gotelli & Rohde 2002). Experimental approaches can focus on a particular factor or factors to clarify mechanisms, but may not adequately reflect complex natural situations in which species interactions are embedded. In contrast,

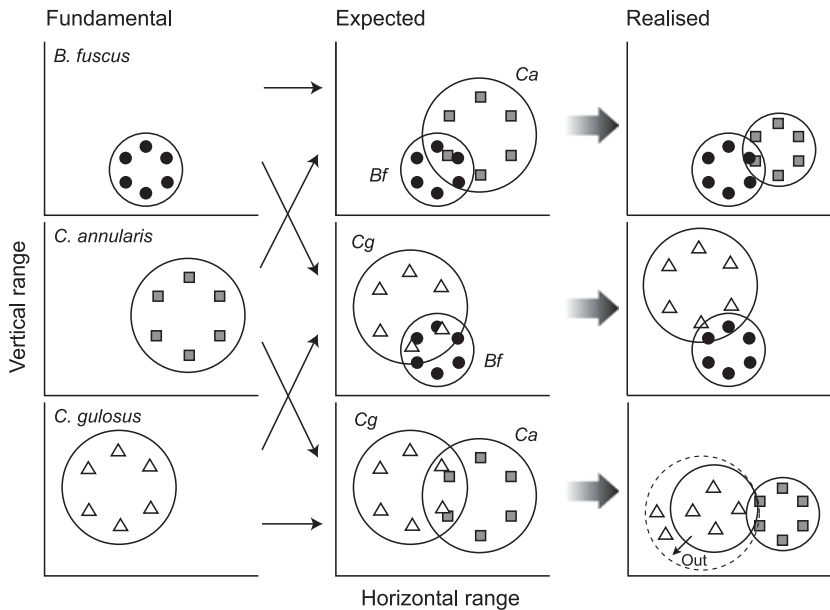


Fig. 8. Schematic diagram showing the fundamental (left), expected (middle) and realised (right) space use of three species and their combinations. Sizes of open circles correspond to space occupancy (proportion of tidepools occupied). Dotted circle show possible realized tidepool occupancy, taking into account the number of displaced individuals.

null model analyses are more effective in revealing unexpected patterns and under situations where experimental approaches are difficult or not feasible and the assumption of conventional statistical tests are violated (Gotelli & Graves 1996; Morin 1999). Construction of appropriate null models, however, is problematic (Colwell & Winkler 1984; Gilpin & Diamond 1984; Gotelli & Graves 1996). Unlike previous studies, our null model used the expected values of spatial occupancy and overlap derived from experiments without intra-/interspecific interaction on different spatial scales. This null model analysis based on experimental results is considered less bias-prone and will allow a more rigorous examination of the pattern of resource utilization and mechanisms of community organization.

The results can be represented in a schematic diagram depicting fundamental and realized patterns of space use (Fig. 8). Most notably, *B. fuscus* showed no difference between fundamental and realized spatial niche, while the two *Chaenogobius* species showed differences. *Chaenogobius annularis* had reduced occupancy under hetero-specific treatments (i.e. with both *C. gulosus* and *B. fuscus*) and its area of use shifted towards the lower intertidal with a stronger tendency of aggregation. In contrast, *C. gulosus* had different responses depending on mixed species. When combined with *B. fuscus*, *C. gulosus* shifted towards the upper intertidal without decreasing its occupancy, leading to a reduced interspecific overlap. With *C. annularis*, *C. gulosus* showed a shift towards the lower intertidal and increased displacement of individuals, suggesting the potential effect of interspecific interactions.

Chaenogobius annularis obviously decreased its occupancy when mixed with *B. fuscus*, while the latter did not show an apparent change. Interestingly, *C. annularis* reduced spatial overlap with *B. fuscus* by aggregating in lower tidepools, suggesting that species interaction may generate vacant space (in this case the upper intertidal) as part of a realized pattern.

In the combination of *B. fuscus* and *C. gulosus*, overlap was reduced not through a decrease in tidepool occupancy but through a shift by *C. gulosus* towards the upper tidal zone. Consequently, the realized total occupancy of *B. fuscus* and *C. gulosus* was greater than the expected combined occupancy of the two species. This demonstrates that the range of fundamental space use may be expanded as well as reduced under the influence of interactive relationship. In other words, species interactions could induce expansion of niche at least on one dimension (i.e. space).

Patterns of species assembly represent a summary picture of the interactions and non-interactions characterizing a particular assemblage of species (Tokeshi 1999). Extrapolation of our experimental results is helpful for understanding the patterns in the field, though care should be taken in considering multi-species situations. *Bathygobius fuscus* mainly occurred in the mid-low intertidal and, together with *C. gulosus*, appeared to have forced *C. annularis* into the lowest zone. *Chaenogobius gulosus* was relatively more abundant towards the upper intertidal, possibly due to the dominance of *B. fuscus* in the mid-low intertidal. In addition, the observed overlap in the field was similar to the realized overlap of tidepool use in the mesocosm experiment. It may be conjectured that there is a common or similar effect of species interaction with regard to space use under both experimental and field conditions. Overall, our results lend support to a view that ongoing competitive interactions work as a driver in the organization of intertidal fish assemblages.

PATTERNS ON DIFFERENT SPATIAL SCALES

Resource use overlap does not directly represent occurrence and/or intensity of competition (e.g. Morin 1999; Munday, Jones & Caley 2001), but differences in overlap between different situations suggest the presence of some forces which

can modify the shape and volume of niche (Tokeshi 1999). Our experiments on different spatial scales revealed different patterns of spatial use overlap even for the same species combination. It is interesting that for all interspecific combinations realized spatial overlap was significantly reduced on the habitat-wide scale (mesocosm experiment) but not on the microhabitat scale (laboratory experiment). Reduction in spatial overlap on the habitat-wide scale mostly resulted from differential tidal height distributions of three gobiids, while on the microhabitat scale relatively high interspecific overlap was partly due to intensive interactions such as chasing and attacking when confined in a tidepool. In contrast, reduction in intraspecific overlap on the microhabitat scale was due to individuals of each gobiid species showing flexible substrate choices under intraspecific conditions, leading to spatial segregation of conspecifics within a tidepool. While conspecific individuals of *Chaenogobius* species used different substrate types to remain in the shelter, under interspecific encounters *C. gulosus* excluded *C. annularis* from the shelter, resulting in the latter's reduction of shelter use (by day, Table 2).

Thus our results indicate that patterns of interaction and spatial utilization vary and different processes of community organization may operate on different spatial scales. Overall, interspecific spatial segregation seems to occur mainly on the habitat-wide scale, while intraspecific segregation is more likely on the microhabitat scale. In this respect, the pattern in the aquarium experiment is considered to represent interactions at low tide (within a tidepool) while the pattern in the mesocosm reflects interactions at low and high tide (within/among tidepools).

The results of growth measurements in the mesocosm experiment suggest that *C. annularis* experienced negative impacts of interspecific interaction on its growth on the habitat-wide spatial scale. In terms of proximate mechanisms, this may have been attributable to (i) direct interspecific competition, or (ii) its indirect effects through greater intraspecific aggregation in some pools resulting in stronger intraspecific competition. These direct and indirect effects of interspecific interactions are not mutually exclusive and our data do not allow their separate recognition. Nevertheless, the mesocosm experiment has confirmed that the negative effect of interspecific competition on growth is larger than that of intraspecific competition.

Environmental variability is generally much larger among tidepools than among microhabitats within a tidepool. Hilton, Wellenreuther & Clements (2008) showed that physiological differences underpin habitat divergence in sympatric congeneric intertidal fishes. This might apply to the present study where reduced interspecific overlap occurred on a habitat-wide scale. Overall, habitat-wide space partitioning seems relatively more important than microhabitat partitioning in a tidepool, as far as small (< 1 m²) and shallow (< 9.5 cm mean depth) tidepools are concerned. Fishes can move between tidepools at high tide while they have to stay in one tidepool at low tide time. Given large environmental variability of tidepools (Metaxas & Scheibling 1993), it is

advantageous to have phenotypic niche flexibility (e.g. Nakano, Fausch & Kitano 1999) allowing the use of different tidepools, especially for competitively inferior species. In addition, species- and size-related microhabitat utilization (Arakaki & Tokeshi 2005) may lessen the negative impact of interactions among intertidal fishes.

COMPETITIVE COEXISTENCE

The present study suggests competitive coexistence in this assemblage forming intricate interspecific relations among fish species but with no absolute dominant in terms of both space use and feeding efficiency. *Bathygobius fuscus* and *C. gulosus* had variable negative impacts on the habitat utilization and growth of other species, while *C. annularis* was generally on the receiving end of influence. The negative effect of interactions on growth apparently worked in an asymmetric manner from *C. gulosus* to other species, while that between *B. fuscus* and *C. annularis* occurred in a symmetric manner. Although a superior competitor for space use, *B. fuscus* seemed to spend much energy in competitive interactions, often resulting in reduced growth. In contrast, *C. gulosus* may feed and grow more efficiently by changing patterns of space use. Thus, the results of the present study point to a possible trade-off between competitiveness and growth efficiency in these fishes, an aspect which is worth investigating further.

The fact that *C. annularis* is apparently an inferior competitor for space raises a question about how it can coexist with competitive superior species in the system. *Chaenogobius annularis*' space use was suppressed by other species, especially *B. fuscus*, though it can potentially use a wider range of tidepools than *B. fuscus* does. In this respect, *C. annularis* may be considered a generalist that can use part of the resource spectrum that is less exploited by specialist species (Wilson & Yoshimura 1994; Olson, Mittelbach & Osenberg 1995). Indeed, *C. annularis* showed varied microhabitat use and a wide range of spatial distribution in the field (Arakaki & Tokeshi 2005). Moreover, *C. annularis* had less continuous use of the same tidepool while *C. gulosus* tended to stay in the same tidepool (Sasaki & Hattori 1969), suggesting that the former has higher mobility among variable habitat patches.

Rosenzweig (1981) pointed out that habitat selection can lead to competitive coexistence with some density-dependent processes. In the present study, varied patterns of habitat selection occurred on different spatio-temporal scales. As tidepools represent periodically 'patchy habitats' (i.e. boundaries disappear at high tide), intensive competition is probably restricted to local, short time scales in tidepools. On the other hand, moving between tidepools also implies associated risks of predation, physical injury and failure to find suitable habitats. Therefore, the balance between the benefits/costs of moving and staying is considered an important aspect of their coexistence. To some extent tidepool fish assemblages may be supported by a process similar to metapopulation dynamics (Gilpin & Hanski 1991; Hanski 1999) whereby individuals

lost from particular tidepools (local extinction) are replaced by those surviving in other habitats (regional maintenance).

Conclusion

Our integrative approach combining experimental and null model analyses revealed the alteration of fundamental spatial niche coupled with a reduction in growth under interspecific interactions. Variable patterns of change in space utilization indicated the operation of scale-dependent processes in intertidal fish assemblages, whereby intraspecific interactions were more evident on a microhabitat scale and interspecific ones on a habitat-wide, mesocosm scale. Field-observed patterns of spatial distribution and overlap matched the experimental results, suggesting that the organization of intertidal fish assemblage is at least partly governed by competitive interactions for space use. Intertidal fishes achieve coexistence by adjusting and modifying their fundamental niches to mitigate the negative impact of biotic interactions in patchy and heterogeneous tidepool environments. The present study has demonstrated that the application of experiment-based null model analysis is an effective tool for clarifying the dynamic aspects of niche and species coexistence.

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