Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors

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While the facilitation–competition paradigm under the stress-gradient hypothesis has received recent attention, its rigorous testing is yet to be explored. Most of the studies have considered a switch in the net interactions from competition to facilitation with increasing environmental stress as primary evidence supporting the hypothesis, though few studies examined changes in interaction along a full range of a stress gradient. Here, we have conceptualized possible variations in the patterns of change in interaction strength along such gradient. Based on this, we empirically evaluated the temporal shift in the interaction between two marine sessile animals, goose barnacles (*Capitulum mitella*) and mussels (*Septifer virgatus*), under multiple stress factors. The net effect of goose barnacles on mussel survivorship was positively related to the total stress gradient encompassing two stress factors, physical disturbance and thermal stress, while no negative value occurred even under mild conditions. When the two stress factors were treated separately, however, the net effect demonstrated apparently different patterns: monotonic increase with physical disturbance versus a quasi-asymptotic pattern (no change over a wide range) with thermal stress. These variable situations have not previously been recognized in this discipline, and the present study emphasizes the importance of an integrative and mechanistic approach to testing and deciphering the facilitation–competition paradigm.

Keywords: facilitation; competition; environmental stress; net effect; stress-gradient hypothesis; species interaction

1. INTRODUCTION

Two opposite processes, facilitation and competition, have been recognized as key drivers in a wide range of natural communities (Bruno *et al.* 2003; Kawai & Tokeshi 2006). The relationship between the harshness of environmental stress and the relative importance of facilitation and competition has been conceptually formalized in the 'stress-gradient hypothesis', predicting that the net negative competitive effects are more important under relatively benign environmental conditions, whereas positive facilitative effects are more important under harsher conditions (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998). Note that the term 'stress' in this hypothesis should be interpreted to mean any environmental factor, the extreme conditions of which have some negative effects on the organisms involved (e.g. heat/desiccation, nutrient level, osmotic pressure, disturbance and grazing, as suggested by Bertness & Callaway (1994)), whereas plant ecologists tend to restrict its reference to some conditions such as desiccation and high temperature. The generality of this hypothesis has recently been under vigorous debate, particularly among plant researchers (Maestre *et al.* 2005, 2006; Lortie & Callaway 2006). The lack of a consistent approach for testing this hypothesis makes it difficult to achieve an integrated view of the relationships between stress gradients and species interaction. Most of the previous studies examined species interactions at only two levels of a stress factor (e.g. Pugnaire & Luque 2001), amounting at most to an estimation of a linear relationship. Clearly, assessment of species interaction under all possible levels of stress is necessary for a better understanding of the relationship (Maestre & Cortina 2004; Brooker *et al.* 2006; Lortie & Callaway 2006).

Conceptually, if a whole range of a stress gradient is taken into account, a system may show a facilitation–competition shift (figure 1*a*), facilitation-only (figure 1*b*) or competition-only (figure 1*c*), with either monotonic increase/decrease (cases (i) and (ii) of figure 1) or non-monotonic changes with a peak in the intermediate levels of stress (cases (iii) and (iv) of figure 1). For identifying these variable relationships, a shift in interaction must be examined along a sufficiently wide range of stress gradients covering both benign and severe conditions for target species. For example, if interaction was examined only along the left half of the stress gradient (under benign conditions) in case *a*(i), the relationship would be indistinguishable from case *c*(i). Likewise, the right half of case *a*(i) cannot be distinguished from case *b*(i). Moreover, the half parts of cases *a*(iii) and *a*(iv) have the same patterns as in cases *a*(i) and *a*(ii). Thus, researchers should be aware of potential misrepresentation and misinterpretation due to
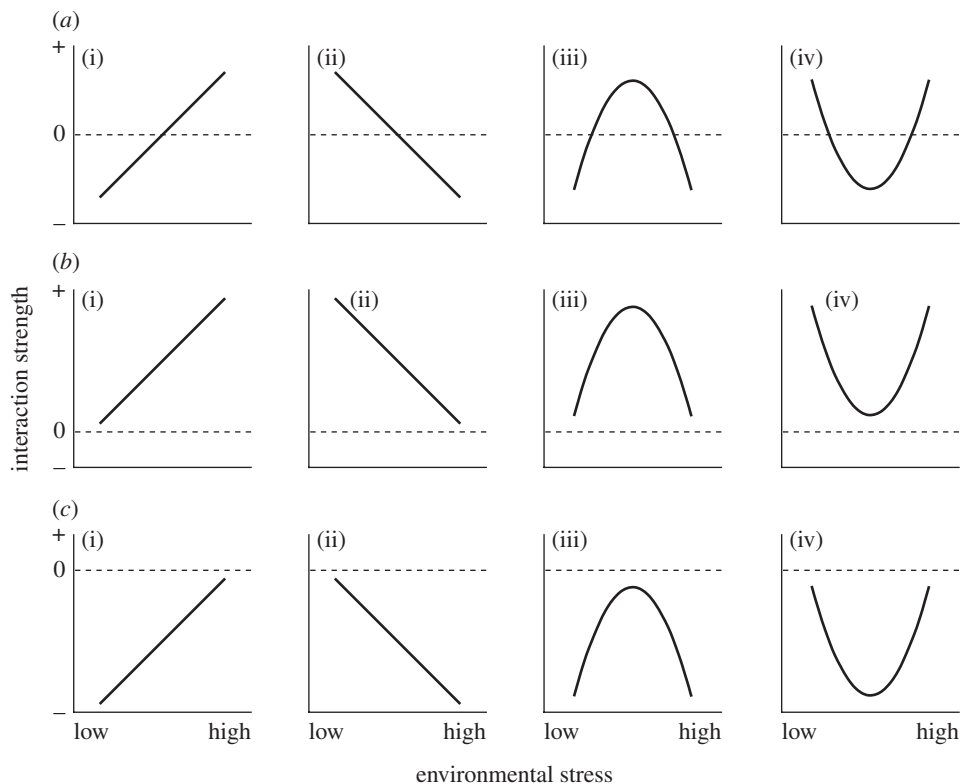
Figure 1. Schematic showing the possible relationships between an environmental stress gradient and the strength of species interaction: (*a*) facilitation–competition shift, (*b*) facilitation-only and (*c*) competition-only, with (i) monotonic increase, (ii) monotonic decrease, (iii) positively peaked and (iv) negatively peaked.

an inadequate assessment of interaction within narrow ranges (Belcher *et al.* 1995; Kadmon 1995; Foster 1999).

In addition to this 'range of coverage' problem for a single stress factor, there is an issue of multiple environmental factors operating simultaneously when one deals with the facilitation–competition paradigm. In natural communities, two or more environmental factors often act at the same time as stresses for a species and may have separate and/or combined effects on the performance of that species, leading to variable relationships as depicted in figure 1. Despite this, most of the previous studies have dealt with the relationship between only one stress factor and net species interaction (e.g. Callaway *et al.* 2002; Maestre & Cortina 2004). Kawai & Tokeshi (2004) demonstrated that on a moderately wave-exposed intertidal rocky shore of Amakusa, southwestern Japan, the goose barnacle *Capitulum mitella* positively influenced the survivorship and growth of the mussel *Septifer virgatus* through amelioration of thermal stress and of physical disturbance caused by wave action. As the magnitude of these stress factors varies temporally in different ways and the tolerance of *Septifer* may differ depending on the factors, *Septifer* is expected to respond to such stress factors differently. Therefore, two different temporal stress gradients for *Septifer* must exist. This implies that the net effect of *Capitulum* on *Septifer* may probably have different relationships with different stress gradients. Furthermore, there is no obvious common unit for these stress factors, making it difficult to compare their harshness even for one species. One possibility is to estimate the harshness of environmental stress by the performance (e.g. mortality, growth or productivity) of each target species, not by the direct measurement of environmental conditions themselves (Grime 1977; Underwood 1989; Goldberg *et al.*

1999; Parker *et al.* 1999; Hastwell & Facelli 2003; Lortie & Callaway 2006).

The present study has aimed at an integrative and mechanistic approach to testing the stress-gradient hypothesis, using the *Capitulum–Septifer* pair as a model system. We have assessed temporal variations in (i) the combined and separate effects of two stress factors (thermal stress and physical disturbance) for *Septifer* and (ii) the net effect of *Capitulum* on *Septifer*. This represents the first attempt to tease apart the effects of multiple stress gradients in animal–animal interactions. In order to achieve this goal, we have employed a series of transplant experiments involving artificial patches separately controlling the effects of different stress factors.

2. MATERIAL AND METHODS

The study was conducted on a moderately wave-exposed rocky shore (32°31′ N, 130°02′ E) of the Amakusa Shimoshima Island, southwestern Japan. A series of artificial patch transplant experiments involving artificial shade or transparent physical barriers were carried out in the upper intertidal zone (2.0–2.5 m above mean lower low water (MLLW)) during February–December 2003. Artificial shade reduced thermal stress only (caused by solar radiation), while transparent barriers reduced physical disturbance only (hydrodynamic forces caused by wave actions; see below). Experiments were conducted six times during the study period, each lasting four weeks.

In each experiment a total of 32 artificial patches were prepared and assigned to the following four treatments (eight replicates each): (i) *Septifer*-only, (ii) *Septifer* with artificial shade, (iii) *Septifer* with transparent physical barrier, and (iv) mixed (*Septifer* with *Capitulum*). Middle-sized *Septifer*
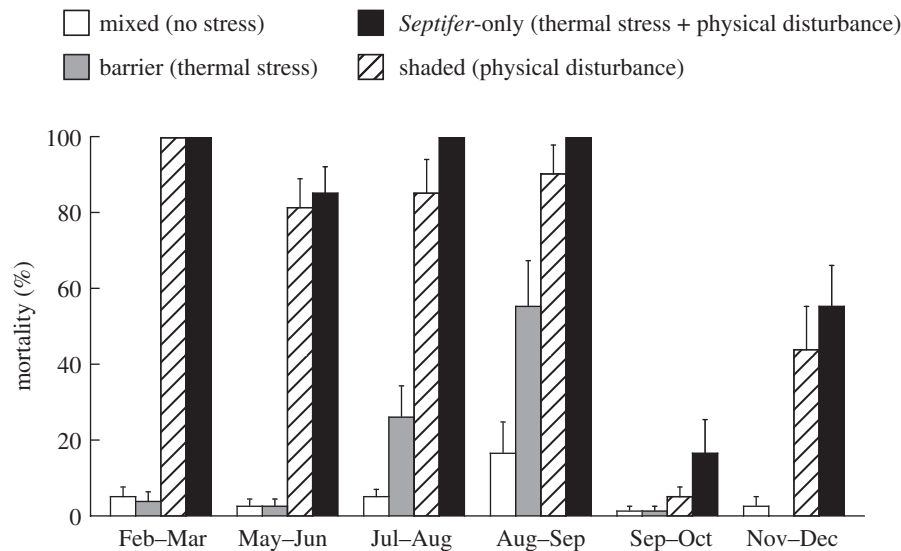
Figure 2. Mortality of *Septifer* in the transplant experiments for six experimental periods ($n=8$ for each treatment). Values are untransformed means $+$ 1 s.e. Stress factors involved are shown in parentheses.

(25–40 mm in shell length, the maximum anterior–posterior axis) and *Capitulum* (10–20 mm in rostral–tergal (R–T) length the length between the rostrum and the tip of the tergum) were collected from the upper intertidal habitats near the transplant site. For the *Septifer*-only, the *Septifer* with artificial shade and the *Septifer* with transparent physical barrier treatments, 10 *Septifer* were placed in the centre of a $10 \times 10 \times 1$ cm ceramic tile and allowed to attach to the tile in the aquarium. For the mixed patches, 16 *Capitulum* were glued in a circle onto a ceramic tile using water-resistant epoxy resin, and 10 *Septifer* were placed within the *Capitulum*-circle and allowed to adjust their positions and attach to the tile and to one another by byssal threads. These tiles were kept in a laboratory running seawater aquarium for one week to allow firm attachment and acclimatization. Each artificial patch except the barrier treatment was covered with a predator exclusion cage ($10 \times 10 \times 5$ cm) constructed of 5×5 mm stainless mesh. This successfully excluded the predatory snails *Morula musiva* and *Thais clavigera*. The barrier patch was covered with a small cage ($7 \times 6 \times 1.5$ cm) made of 5×5 mm stainless mesh for preventing *Septifer* from being dislodged or damaged by wave action, but not protected from thermal stress. The shaded treatment involved coverage by a 10×10 cm double-layered canopy of white plastic screen (0.5×0.5 mm mesh) attached to the top of the cage to reduce solar radiation, but not physical disturbance. After all the mussels had attached firmly, the tiles (patches) were taken to the field and randomly placed on rock surfaces using stainless steel screws on a slightly sloping flat rock in the upper intertidal. Patch positions were randomized at the start of each experiment and all patches were removed at the end of each experiment. The mortality of *Septifer* was monitored for an experimental period of four weeks; this experimental period was considered appropriate, as the thermal stress fluctuated on an approximately monthly basis at this site (Arakaki & Tokeshi 2006). Parts of this experiment (*Septifer*-only and mixed treatments) were identical with those in our previous work (Kawai & Tokeshi 2006).

The harshness of stress factors for *Septifer* was quantified by the performance (i.e. mortality) of *Septifer* in the barrier treatment (thermal stress only), the shaded treatment (physical disturbance only) and the *Septifer*-only treatment

(combined stress). The net effect of *Capitulum* was estimated as the difference in the performance (survivorship, the reciprocal of mortality) of *Septifer* between the mixed situation with *Capitulum* and the single situation using the log response ratio, lr (Gurevitch & Hedges 2001). The effect of each stress factor on the mortality of *Septifer* was tested using a three-way ANOVA, with physical disturbance and thermal stress as fixed factors and time as a random factor. This was based on the results that neither physical disturbance nor thermal stress had a significant negative effect on *Septifer* under the mixed situation with *Capitulum* throughout the year (see §3). To evaluate the relationship between the stress gradients expressed as temporal variation in the mortality of *Septifer* and the net effect of *Capitulum*, regression analysis was conducted. All statistical analyses were performed with the SPSS v. 11.5.1 package (SPSS, Inc.).

3. RESULTS

Stress factors for *Septifer* showed large temporal variations (0–100% mortality; figure 2). Mortality in the *Septifer*-only treatment was low (approx. 15%) in early autumn and intermediate (approx. 50%) in early winter, but was very high (90–100%) in all other seasons. In contrast, almost all *Septifer* survived in the mixed treatment with *Capitulum*, indicating no stress for mussel survivorship. Two stress factors showed different temporal patterns; physical disturbance was very strong all year round, except from early autumn to early winter, while thermal stress was substantial only in midsummer. There was no interaction between the two stress factors, suggesting that these stresses had additive effects on the mortality of *Septifer* throughout the year (table 1).

The net effect of *Capitulum* had a monotonically increasing relationship with the total stress gradient encompassing physical disturbance and thermal stress (figure 3a). However, no effect showed significantly negative values even under the mildest condition. Considering the net effect along two different stress gradients separately, it showed different patterns with different stress gradients (figure 3b,c). The net effect positively scaled with the harshness of physical disturbance (figure 3b), indicating a pattern similar to the total

Table 1. Results of a three-way ANOVA on the mortality of *Septifer* in a series of transplant experiments, with physical disturbance and thermal stress as fixed factors and time as a random factor. (Data were arcsine (square root) transformed before the analysis.)

source of variation	d.f.	F	p
physical disturbance (p)	1,5	25.444	0.004
thermal stress (t)	1,5	4.945	0.077
time	5,5.36	2.034	0.219
$p \times t$	1,5	0.001	0.979
$p \times$ time	5,5	14.608	0.005
$t \times$ time	5,5	1.647	0.299
$p \times t \times$ time	5,168	1.650	0.150

stress gradient (figure 3a). In contrast, the net effect had a quasi-asymptotic relationship with thermal stress (figure 3c), departing from the pattern observed for the total stress gradient (figure 3a).

4. DISCUSSION

Conceptualization of possible relationships under the stress-gradient hypothesis (figure 1) is considered useful, as the hypothesis lacks an integrated view of what patterns are to be expected and tested. Recent reviews (Maestre *et al.* 2005; Lortie & Callaway 2006) evaluating the predictability of the stress-gradient hypothesis have considered a significant switch in the net interactions from competition to facilitation with increasing environmental stress as primary evidence supporting the hypothesis. However, it should be pointed out that, without examining the patterns of change in interaction along the stress gradient, differences among cases *a*(i), *a*(iii) and *a*(iv) of figure 1, for example, cannot be detected. Furthermore, changes in interaction strength without a facilitation–competition shift (figure 1*b,c*) are also possible. Indeed, our study has experimentally demonstrated a monotonically increasing relationship between the total stress gradient for *Septifer* covering a wide range (16–100% mortality in average per month) and the net effect of *Capitulum* on *Septifer* in the positive range of interaction (figure 3a). The strength of the facilitative effect of *Capitulum* on *Septifer* survival increased with increasing environmental stress on the temporal scale, while competitive effects never appeared even under mild conditions, coincident with case *b*(i) in figure 1.

Liancourt *et al.* (2005) suggested that a species having both low tolerance to a particular environmental stress and a strong competitive-response ability is likely to benefit from other species without receiving competitive effects. *Septifer* with a faster growth rate (15 mm yr^{-1} in shell length; Morton 1995) and low tolerance of both thermal stress and physical disturbance may fit this picture. In addition, a potentially low competitive ability of *Capitulum* with a slow growth rate (2 mm yr^{-1} in rostral–carinal length; Nakamura & Tanaka 1995) may also have contributed to the present observation. However, it is still uncertain whether such a monotonically increasing relationship within the positive range (case *b*(i) of figure 1) is common among natural communities. Callaway *et al.* (2002), in one of the few studies where sufficient data were gathered for this type of analysis, found an asymptotic
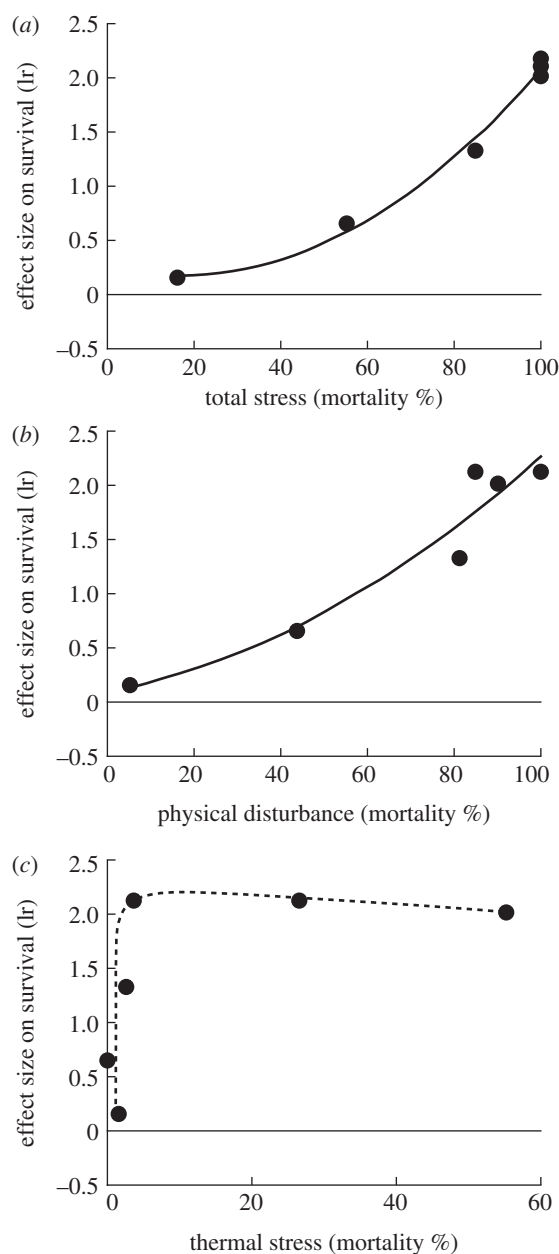

Figure 3. Relationships between the stress gradients and the net effect of *Capitulum* on the survivorship of *Septifer*. (*a*) Total stress expressed as the mortality of *Septifer* in the *Septifer*-only treatment versus the net effect of *Capitulum* ($y=0.229-0.008x+0.00027x^2$, $R^2=0.99$, $p=0.0008$). (*b*) Physical disturbance expressed as the mortality of *Septifer* in the shaded treatment versus the net effect of *Capitulum* ($y=0.093+0.008x+0.00014x^2$, $R^2=0.93$, $p=0.0202$). (*c*) Thermal stress expressed as the mortality of *Septifer* in the barrier treatment versus the net effect of *Capitulum* (a dashed line fitted by eye).

relationship in alpine plant communities. The importance of the facilitative effect of plants on neighbours increased towards an asymptote with environmental harshness (left half of case *a*(iii) of figure 1). Brooker *et al.* (2006) demonstrated another case in which heather had a facilitative effect on pine saplings through mitigation of deer browsing impact, particularly at the intermediate levels of grazing, resulting in a hump-backed relationship between the facilitative effect and grazing pressure (case *b*(iii) of figure 1). In this circumstance, the potential for heather to hide the saplings was reduced in areas with high
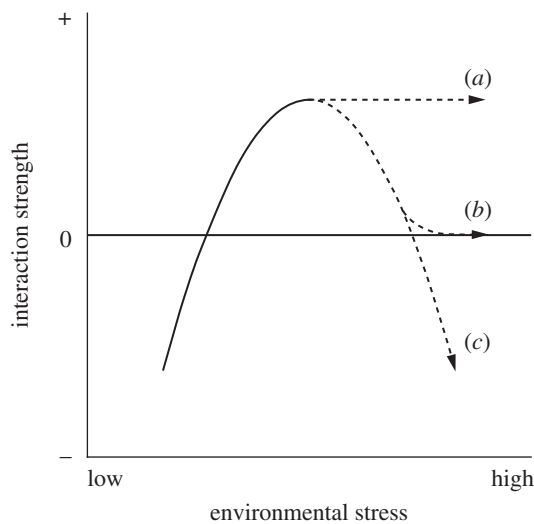
Figure 4. Schematic showing possible variation in the relationship between an environmental stress gradient and the strength of species interaction under harsh environmental conditions. Facilitative effect may (*a*) reach an asymptote, (*b*) decline to a neutral level or (*c*) turn into a negative value (competitive effect) with increasing environmental stress.

deer density due to increased foraging. In general, the importance and/or intensity of facilitative effects may reach an asymptote (figure 4*a*) or even decline (figure 4*b*) with increasing environmental stresses, probably because facilitators are less successful in ameliorating stress factors and promoting the survival of facilitated species under very severe environmental conditions (Michalet *et al.* 2006). Furthermore, if stress factors coincide with resource factors for both the facilitator and the facilitated species, such as water for plants, competitive effects may manifest under extremely severe conditions (Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Michalet 2007; figure 4*c*). In addition, different main stress factors among studies (e.g. disturbance, this study; low temperature, Callaway *et al.* 2002; grazing, Brooker *et al.* 2006) may also lead to variation in the shape of the relationship. More empirical and theoretical work examining not only the switch in interaction but also the whole shape of relationship under various stress factors will be needed for a comprehensive testing of the stress-gradient hypothesis.

In our study site, two stress factors, physical disturbance and thermal stress, had a significant influence on the performance of *Septifer*, showing different temporal stress gradients (figure 2). Considering these two stress gradients separately, the net effect along the gradient of thermal stress revealed a quite different pattern from that along the gradient of physical disturbance (figure 3*b,c*). The net effect of *Capitulum* involves two different stress-ameliorating functions, amelioration of thermal stress and of physical disturbance (Kawai & Tokeshi 2004), suggesting that the gradient of each stress factor particularly thermal stress in this case may not solely explain the shift of the net effect. These results suggest that consideration of the net effect along just one particular stress gradient may be misleading.

Most of the previous studies have dealt with only one environmental condition such as precipitation or temperature as an indicator of environmental harshness (e.g. Tielbörger & Kadmon 2000; Callaway *et al.* 2002;

Maestre & Cortina 2004; Kikvidze *et al.* 2005). Although Maestre & Cortina (2004) used variation in precipitation among sites as a spatial stress gradient, the survivorship of *Pistacia* without tussock grass neighbours did not show a monotonic change with the precipitation level. Other factors could possibly have had a large influence on shrub survival, suggesting that examining the relationship between the net effect and precipitation would not be sufficient for testing the stress-gradient hypothesis. Non-monotonic relationships between the net effect and one stress gradient revealed in the study by Maestre & Cortina (2004) and in this study (figure 3*c*) may imply the involvement of other stress factor(s).

Several kinds of stress factors usually influence facilitated species and the net effect of facilitators may also include multiple habitat-modifying functions as well as competitive effects. Consequently, for a rigorous testing of the stress-gradient hypothesis, the relationship between the net effect encompassing multiple components and the total stress gradient should be examined. We suggest that the performance of organisms, such as productivity, growth and survivorship, under the single-species situation may be used as a surrogate for the harshness of the combined stresses. However, it should be noted here that sensitivity to environmental stresses often differs among these performance measures. For quantifying stress gradients, growth or productivity with potentially high sensitivity to stress factors may be effective under benign environmental conditions, while survivorship with relatively lower sensitivity may be adequate under harsher conditions. Improvement in our understanding of the relationship between species interaction and stress gradients through an integrative and mechanistic approach as used in this and our previous studies (Kawai & Tokeshi 2006) is considered crucial for making reliable predictions about the possible changes in community structure under variable environmental conditions, particularly in the scenario of ongoing climate changes (Harley *et al.* 2006).

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