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Stress Gradient Hypothesis: do animals facilitate each other during stressful times?

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Abstract
Interactions among organisms can be a major force structuring biotic communities. The focus among biologists was long aimed at competition and negative interactions. Lately more evidence and attention are directed at facilitation and positive interactions. The Stress Gradient Hypothesis (SGH), which states that individuals will facilitate each other more under stressful situations, has been proven for plant-plant interactions. Is this theory also applicable to animals? To answer this question I've done a literature study. To help answer this question I've divided the animals into three groups: mollusks, arthropods and mammals. The articles found, provide evidence for the applicability of the SGH on mollusks. Evidence for arthropods and mammals is not as clear. The studies also have some concerns making them generally applicable. Thus I conclude that more and above all longer studies need to be done on this subject to provide unsurpassed evidence either in favor or against the applicability of the SGH on animals.

Introduction
Interactions among organisms can be a major force structuring biotic communities (Arthur & Mitchell 1989). The theory has long been that competition is the main source on species interactions and the resulting community structures. With decreasing resources, species will fight, directly or indirectly, for the remaining ones. The strongest species will get the most resources and will be better in providing for his offspring. Those with more and stronger offspring will get more of their genes in the next generation. Long biologists have thought that species mostly influence each other through negative interaction. Recently more and more studies show that this might not be the case.

In 1994 a study was published by Bertness and Callaway that showed that positive reactions also had an effect on the survivability of individuals. They showed that facilitation, to ameliorate an environment for another individual, also is a driving force in species-species interaction. Positive interactions were defined by them as all non-consumer interactions between two species that have a positive effect on at least one of the species involved. They produced a theory, that states that with increasing levels of stress, competition becomes less important and facilitation becomes more important (see Fig 1.). Stress forces an individual to expend energy on other fields than reproduction. Simply said, species rather help each other survive harsh conditions, such as drought, salinity, heat, disturbance and low nutrient levels, instead of fighting over the remaining resources. This theory is known as the Stress Gradient Hypothesis (SGH) and has become an important framework within ecology over the last twenty years (Santiago *et al.* 2014). The SGH is studied for plants but not so much for animals. Should this theory only apply for plants or can we use it on animals as well? Animals can handle abiotic stress differently than plants. Plants cannot go somewhere else when they run out of a certain resource, while animals are capable of doing so. Is the SGH only applicable on plants or is there proof that animals act according to this theory?

To answer this question I've done a literature study. I've searched databases (Picarta and Web of Science) for articles using the term SGH. This showed thousands of hits, mostly of research done on plants. To narrow the search I added the word animal to my search frame. This produced less hits, but included still a lot of research done on plants. Amidst these articles I found 4 useful articles about arthropods. In addition, I used the article of Barrio *et al.* (2013) to find related articles on mammals and mollusks.

In the following I will present the results of this literature survey. I will first present studies done on mollusks, followed by studies on arthropods and last studies done on mammals. After this I will discuss the generalities or dissimilarities between these groups and also where the results deviate from the original SGH for plants. In the discussion I will discuss the problems that these studies face and which improvements can be made to further research that I think is needed.

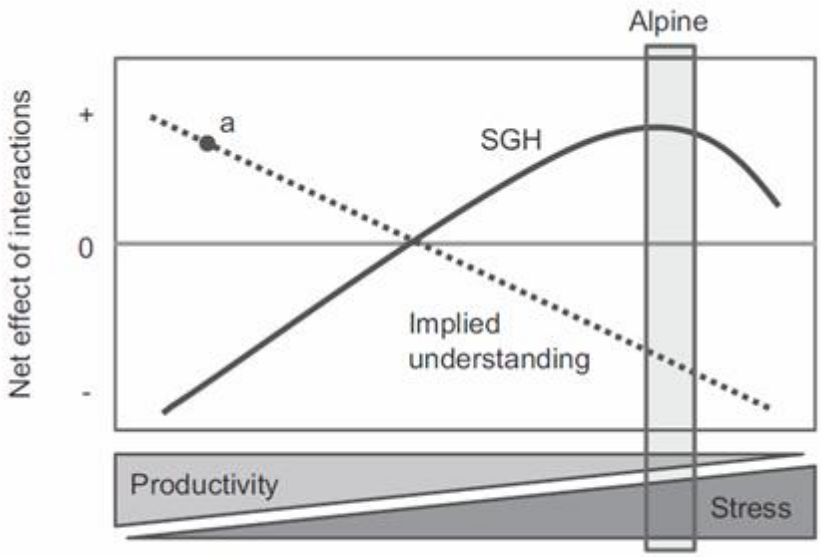

Figure 1. Stress Gradient Hypothesis. With increasing stress levels the net effect of interactions changes, from net negative to net positive. Against implied understanding which says interactions go from net positive to net negative. When productivity is lowest and stress levels highest the net interactions shift to 0, indicating almost no more interactions.

Mollusks

The first group of animals I will discuss are mollusks, because they are the most easy to compare to plants. Just like plants, many mollusks are unable to move away from a stressed environment. This means they need to find other ways to deal with their stress. Stress is caused by two factors, waves causing disturbance stress and the sun causing thermal stress. Will mollusks facilitate each other during stressful times?

Kawai and Tokeshi published studies in 2006 and 2007 on this subject. They looked at goose barnacle *Capitulum mitella (*Scalpelliformes) and the mussel *Septifer virgatus (*Mytiloida*)*, both belonging to the phylum of *Mollusca* (mollusks). They hypothesized that *Capitulum* would help *Septifer* cope with physical disturbance and thermal stress, while *Septifer* would provide a place to grow for the *Capitulum*. When they separated these stress factors there was no clear indication of facilitation. By keeping *Capitulum* and *Septifer* apart from each other they saw that *Septifer* had mediocre mortality rate (50%) in the winter, but extreme high mortality rate in the other seasons (90-100%). When combined with *Capitulum* and both stress factors are present there were almost no casualties of *Septifer*, indicating that there's indeed facilitation. They found that with increasing stress levels *Capitulum* would facilitate *Septifer* more and better thus proving that the SGH is applicable on mollusks (Kawai & Tokeshi 2006/2007).

Arthropods

Arthropods are the second group that I will discuss here. Unlike plants and most mollusks (see previous chapter) most arthropods can easily find another location. I've taken it for a fact that they are able to search for another spot when their current one gives a lot of stress. Can facilitation be of great influence on these animals as well?

Most found studies were done on filter feeders, some were done on Plecoptera, some on Coleoptera and others on Trichoptera. In a research done on mosquitos *Ochlerotatus triseriatus* (Diptera*)* and scirtid beetles a significant interaction was found. The beetle provides *Ochlerotatus* with fine particles that it needs for feeding. When posed with stress, in this case less leafs, *Ochlerotatus* gets even more dependent on the scirtid beetle and thus provides evidence for the SGH (Daugherty & Juliano 2002). A second study was done on another filter feeder: caddisflies (Trichoptera). When three species of caddisflies where placed together instead of a single species, the amount of fine particles consumed went up by 66% (Cardinale *et al 2002*). This difference was shown in the lower parts of the stream where in the upper part there is almost no difference. The lower parts of the stream had more disturbance than the upper part. This disturbance prevented the more competitive species to completely take over (Cardinale & Palmer 2002).Thus this study shows that these arthropods facilitate each other and therefore show evidence towards the applicability of the SGH on animals.

However, not all studies on arthropods found evidence for the SGH. McKie *et al.* (2009) showed that increasing species richness and stress levels gave no cause for more facilitation. They even found that more species had a negative effect on the productivity of some of the species.

Mammals.

Mammals are the last group of animals discussed in this thesis. Most studies were done on livestock, for they are abundant, easy to study and researchers want to know the effect of increased grazing on plants, animals and the environment (Biondini *et al.* 1998, Schuman *et al. 1999,* Austrheim *et al.* 2007, Smit & Verwijmeren 2011).
Austrheim *et al.* (2007) showed that sheep facilitate rodents. The sheep had a preference for certain plants to graze on and this provided room for other plants that the rodents use for feeding. When the sheep were experimentally removed, by using an exclosure experiment, the rodents population would suffer. When increasing the food web, by adding wolves, the dependence of one species on another continued. These species kept each other in balance. In the event of a take-over by one of these three (sheep, rodents or wolves) the situation became unstable and caused the demise of all three species (Vial *et al.* 2011). These studies show that there is facilitation between these different kind of mammals and thus evidence for the applicability of SGH on mammals.

Forsyth & Hickling (1998) did a research on the interaction between tahr (*Hemitragus jemlachicus)* and chamois (*Rupricapra rupricapra),* two kinds of goats. This showed that not all interaction between mammals are positive. They showed that there is interspecific competition for the same food sources between these two species and that the only reason they co-exist is because of the increased hunting of tahr, which gave chamois a chance to live there. Thus showing that these mammals don't facilitate each other and providing no evidence for the SGH.

Discussion

Animals differ in many ways from plants. They handle stress in different ways and because of this it is hard to judge if the SGH is applicable on animals. The studies done on mollusks suggest that the SGH applies to this animal group. However, the SGH seems less applicable when looking at animals that are more mobile. Some arthropods (Cardinale & Palmer 2002) and mammals (Austrheim *et al.* 2007) seem to follow the predictions from the SGH but evidence for the opposite has also been found (McKie *et al. 2009,* Forsyth & Hickling 1998). The evidence in favor of the SGH is still delicate. There are trends that might produce something, but maybe not. Facilitation is however more important than biologists believed for a long time. I recommend that further studies need to be done (see last paragraph).

I found very few studies done on animals in relation with the SGH. Most research is done on mammals. This may not be surprising since mammals are for humans directly the most interesting group. We feel most connections with these animals because of cattle, pets, but other groups should not be less important. With the growing food scarcity insects might soon be the new veal (MacEvilly, 2000, Rumpold & Schlüter 2012) and to be able to use them to the fullest we need to know as much as possible of them.

There were some problems with all the studies that might have influenced the results. My first concern is with the length of all studies. Most studies are over the course of a year, sometimes two, but that time frame is too short. Especially researches done over a year are easily influenced by seasonal or yearly fluctuations that produces variable results that need to be carefully looked at. When looking at the graphs produced by Kawai and Tokeshi (2007) it shows a large dip in the otherwise positive growth of both

species. Is this normal for the population to stop growing in this period or is this a onetime event that only had an impact on this study? Longer studies should take away these fluctuations and should get a better controlled result.

This whole thesis is about abiotic stress. However, the original SGH considered both abiotic stress (drought, salinity, heat, disturbance and low nutrient levels) and consumer pressure (predation and herbivory). Facilitation is something that might also work for biotic stress (see Bêty *et al* 2002). Groups of animals are known to watch out for common predators and thus facilitate each other. If the stress increases - for example more predators - the facilitation between prey might also increase and thereby proving the SGH. This has been studied and proven on flocks of birds in India and recently published (Sridhar, H & Shanker, K. 2014). Studies in the field of behavioral ecology might find this theory a useful addition to their collection.

To find out if the SGH is really a useful theory new studies need to be done. These studies need to focus on the long term benefits of facilitation. This means a longer study done over the course of at least two years. This is to prevent yearly or seasonal fluctuation from influencing the results. These studies can be done on abiotic stress, but facilitation against predators is a new and interesting field. I would suggest doing studies on other groups of animals than mammals. A lot is unknown and thus a lot can be learned.

Evidence of SGH / Species	In favor	Against
Mollusks	*Capitulum* facilitate *Septifer* by giving it protection against stress in the form of heat and disturbance .	
Arthropods	Scirtid beetles facilitate *Ochlerotatus* by providing fine particles.	McKie *et al*. (2009) showed that increasing stress gave no more facilitation.
Mammals	Sheep facilitate rodents by eating specific plants which give rodents favored plants room to grow.	*Hemitragus* and *Rupricapra* compete for the same resources.

Figure 2. Evidence in favor or against the SGH. Mollusks are the only group where the SGH seems applicable. Arthropods and mammals still need to be studied a lot more.

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