Competition asymmetry with taxon divergence

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Most organisms experience competition for resources, probably most of the time. As the structure and requirements of closely related species are generally liable to be more similar than in distantly linked species, Darwin suggested that the potential for competition was greater in the former. Since that time, studies have concentrated on interactions of either conspecifics or congeneric species. Shared critical resources, which organisms compete for, are generally mates, food and space (for access to the former). Whilst mates are valued only within species, in that the definition of a species requires it so, both food and space have the potential to be shared by very different organisms. It is now clear that vertebrates may compete with remotely related species: e.g. with squid for krill and with insects for nectar or seeds. Diamond suggested that (i) mutual aggression, (ii) displacement and (iii) evolutionary change in morphology would be increasingly asymmetric with competitor dissimilarity. Thus, with increasing taxonomic distance between two competitors (A and B), increasing aggression is exhibited between them and, increasingly, one consistently displaces the other. Here, Darwin's suggestion and Diamond's first two theories are tested across a taxonomic spectrum for the first time to the best of the author's knowledge. The proportion of spatial competitors in two different marine invertebrate groups demonstrating mutual aggression and displacement increases with taxon divergence (Nei's genetic identity). Congenerics were twice as likely to fight as conspecifics, and confamilial competitors were three times as likely to fight as conspecifics. This relationship seems robust to taxonomic and environmental variability. Competitors do not need to be as distant as birds and bees for complete asymmetry, a different family seems sufficient.

Keywords: interference competition; relatedness; Darwin; bryozoans

1. INTRODUCTION

Competition is probably experienced by all organisms at some point, and by many throughout their lives, and is much debated as a force for shaping observed evolutionary and ecological patterns. Since Darwin (1859), among others, suggested that the potential for competition was greater in more closely related organisms, studies have largely focused on conspecific or congeneric specific battles for space, food or (for conspecifics only) mates. After more than a century of intense investigation, many studies have now demonstrated competition in closely related organisms across a wide range of taxa, on many scales in time and space. More recently, it has been shown that very distantly related animals can be intense competitors (Brown & Davidson 1979; May *et al.* 1979; Woodin & Jackson 1979; Schluter 1986). Perhaps the most obvious example of a competition between distantly related competitors for a common resource is that between vertebrates and various invertebrates, such as between cetaceans and squid for krill (May *et al.* 1979), birds and insects for nectar (Schluter 1986) or rodents and insects for seeds (Brown & Davidson 1979). Man competes with a wide range of taxa for food, with highly asymmetric outcomes (Furness 1982) although, in contrast, such harvesting may release yet more dissimilar species from the effects of competition (Barnes 2001). Competition between distant taxa is not restricted to vertebrate or even animal involvement (Hochberg & Lawton 1990): battles for space on coastal rock are evident between conspecifics and between representatives of different kingdoms (figure 1). So, if competition occurs regularly between competitors of varying

relatedness, Darwin's original ideas and asymmetry of outcome should be testable.

Diamond (1987) suggested that a number of features of organism encounters would become increasingly asymmetric with competitor dissimilarity (relatedness). He suggested measuring the frequency of mutual aggression, displacement (removal of one competitor by the other) and evolutionary change in morphology. Comparing competition across a spectrum of relatedness is, however, problematical for many reasons. Foremost is that few phyla are composed of many classes, each of which comprise many orders and so on down to species level. In only a few of those that are, does competition for a resource occur regularly across all such taxonomic boundaries. Organisms that are sessile colonizers of the land (plants) and shallow waters (algae and animals) probably provide the best opportunities, as they are often involved in intense competition for a most limiting resource: space. Spatial encounters, leading to aggressive interactions, between marine invertebrates on hard substrata (figure 1) are commonplace (e.g. Connell 1961*a,b*). This study evaluates the first two theories across a taxonomic spectrum for the first time to the best of the author's knowledge. The aim of this study was, therefore, to test the idea of Darwin (1859) and the hypothesis of Diamond (1987) that competitors of increasing taxonomic divergence had increasing asymmetry in their frequencies of displacement. In other words, with increasing taxonomic distance between competitors A and B, increasingly either competitor A consistently displaces competitor B or vice versa. The first hypothesis of Diamond (1987), that competitors of increasing taxonomic divergence also demonstrate increasing mutual

aggression, was also investigated. Thus, the spatial encounters of two groups of marine invertebrates, bryozoans and ascidians, reported in the literature were analysed. Taxonomic divergence was measured both categorically (species, genus, family, superfamily, suborder, order, class and phylum) and linearly (for species, genus and family) using Nei's genetic identity (Thorpe 1982).

2. MATERIAL AND METHODS

(a) *Data collation*

Data on competition for space by two different groups of animals, bryozoans and ascidians, were assembled as separate datasets. Only data from a narrow latitudinal range were used as a relationship has been established between the outcomes of competition and distance from the Equator (Barnes 2002). Data for the bryozoans were collated from the literature from two contrasting regions: 47–60° North and 47–60° South. Despite being of similar latitude, these areas have strong differences in isolation, climate and ecology. The studies encompassed in the northern region were essentially temperate Europe whilst the studies in the southern region were subantarctic and outlying Antarctic islands. The literature used often describes competition for space as intense but confined to particular areas (such as the undersurfaces of boulders). So although total space was not always limiting, certain parts of the hard substrata were. Within each group of animals two datasets were constructed from the appropriate literature (Stebbing 1973; Grosberg 1981; Quinn 1982; Russ 1982; Schmidt & Warner 1986; Lopez Gappa 1989; Turner & Todd 1994; Nandakumar 1995; Barnes & Dick 2000; Maughan & Barnes 2000; D. K. A. Barnes, unpublished data) on the frequency of mutual aggression and overgrowth of a competitor. The outcomes of more than 10 000 interactions between 30 species of bryozoan, and more than 700 interactions between 13 species of ascidian were used.

The main hypothesis (hypothesis number two of Diamond (1987)), that competitors of increasing taxonomic divergence show increasing asymmetry in their frequency of displacement, was examined by measuring the frequency of one competitor consistently displacing the other, i.e. the outcome was consistent in one direction. Displacement was scored in cases of more than 5% overgrowth in accordance with the literature used. It is appreciated, however, that some organisms (particularly including the study groups) may regenerate if the overgrowing competitor later recedes (Todd & Turner 1988). All studies used similar definitions of overgrowth versus tied outcomes. Tied outcomes (that is either mutual, but equal, overgrowth or skeletal build-up but no overgrowth; lack of competitor displacement) do appear to be temporally stable and thus represent a genuine alternative to overgrowth (Sebens 1986; Tanaka & Nandakumar 1994; D. K. A. Barnes, personal observation).

The first hypothesis of Diamond (1987), that mutual aggression would increase between competitors of increasing taxonomic divergence, was investigated by measuring the formation of aggressive structures or attempted overgrowth by competitors.

All meetings between competitors were categorized as within either species, genus, family, superfamily, suborder, order, phylum or kingdom (only species, genus and family data were collated for ascidians). Taxonomic categories were used only if they were represented by at least 15 competitor pairings, and competitor pairings were used only if they were represented by at

least 15 interactions. A potentially confounding factor influencing outcomes of intraspecific meetings between competitors was the possibility of competitors being genetically identical, despite being physically separate. The possibility of scoring encounters of such a nature (which often result in fusion of competitors—homosyndrome) was reduced by recording the results only of encounters between bryozoan colonies that each had an ancestrula present (ancestrulae are sexually produced initial zooids from which colonies are budded).

(b) *Data treatment*

ANOVA and *post hoc* Tukey's tests were performed on the original data of (i) displacement and (ii) mutual aggression, comparing all taxonomic levels. These data were plotted for bryozoans from both regions using a categorical *x*-axis with each taxonomic rank as a category. As plots in both regions established little or no relationship above a specific taxonomic level, arithmetic means (and standard errors) were computed only for data of the lower taxonomic levels (species to family). These data were then fitted to a scale of Nei's genetic index generalized for all taxa. A review of genetic differentiation by Thorpe (1982) provides generalized genetic relatedness data and mean values of 0.273, 0.54 and 0.96 for family, genus and species levels, respectively. These values for generalized Nei's genetic index were used in this study for axis scaling. The peaks of Nei's genetic index are robust to most taxonomic groups, and neither bryozoans nor ascidians are known to differ significantly from generalized peaks (Thorpe 1982). Although the shapes of the peaks, particularly for family and species levels, are not normal, the exact placement of family-, genus- and species-level differences is not important and would not greatly affect the analyses carried out here. First-order regressions were fitted to the competition data in the lower taxonomic levels plotted against Nei's genetic index and associated ANOVA was performed.

3. RESULTS

In testing the core hypothesis of increasing asymmetry in displacement with increasing taxonomic divergence, it was found that the second prediction of Diamond (1987) was supported. The proportion of spatial-competitor pairs demonstrating displacement did, therefore, increase with taxon divergence in bryozoans (figure 2). Despite substantial variability in both 47–60° North and 47–60° South bryozoan datasets at all taxonomic levels, strong and similar trends were apparent (figure 2). In temperate bryozoans the majority (55–100%) of competitor pairs at within-phylum or within-kingdom level showed consistent displacement of one competitor by the other, whilst this occurred in only a minority (all values less than 50%) of conspecific space competitors. Thus, the proportion of temperate bryozoan competitors that were consistently displaced did increase with taxonomic divergence (ANOVA, d.f. = 7,190, $F = 57.1$, $p < 0.001$). *Post hoc* Tukey's tests showed no significant differences between competitors at within-kingdom, -phylum, -order, -suborder and -superfamily levels (all $p > 0.05$) but outcome asymmetry at these levels did significantly differ from that in confamilial, congeneric or conspecific competition (*post hoc* Tukey's tests, all $p > 0.05$). In addition, outcomes of confamilial, congeneric and conspecific competition were all different from each other (*post hoc* Tukey's tests, all $p > 0.05$).

A similar pattern of decreasing frequencies of displacement with increasing taxonomic relatedness was present in Antarctic bryozoans (ANOVA, d.f. = 7,168, $F = 21.3$, $p < 0.001$). *Post hoc* Tukey's tests showed that within-kingdom, -phylum, -order, -suborder, -superfamily and confamilial competition did not significantly differ from each other (all $p > 0.05$) but did differ from the outcomes between congeneric or conspecific competitors (*post hoc* Tukey's tests, all $p > 0.05$). This was subtly different from the temperate-bryozoan results: only within-kingdom outcomes differed from confamilial outcomes in Antarctic bryozoans. Outcome asymmetry in congeneric and conspecific competition was, in Antarctic (as well as temperate) bryozoans, different between groups (*post hoc* Tukey's tests, all $p > 0.05$). Overall, therefore, it can be stated that a trend of increasing displacement with taxonomic difference exists in bryozoans across environments. The proportion of ascidian competitors that demonstrated displacement also increased with increasing taxonomic divergence (figure 2b). The phylogenetic relationship between bryozoans and ascidians (phylum Chordata) is debatable and difficult to establish but unlikely to be close. It is, therefore, suggested that the trend reported is robust to different taxa as well as different environments. The probability of overgrowth in both bryozoans and ascidians more than doubled from conspecific to confamilial competitor pairs.

The first prediction of Diamond (1987), that competitors would show increasing mutual aggression with increasing taxonomic divergence, was also supported. Mutual aggression between competitors did decrease with increasing bryozoan relatedness (figure 3). Most within-phylum or within-kingdom competitors showed mutual aggression, whereas few (only one example greater than 50%) conspecific space competitors did. High but similar levels of variability between competitor pairs were present at all taxonomic levels, but similar trends emerged with respect to northern and southern datasets of both mutual aggression and displacement. There was a significant change in the proportion of competitors showing mutual aggression with taxonomic relatedness in temperate bryozoans (ANOVA, d.f. = 7,199, $F = 45.8$, $p < 0.001$). The outcomes of within-kingdom through to within-superfamily competition were insignificantly different (*post hoc* Tukey's tests, all $p > 0.05$) from each other but were significantly different from those between confamilial, congeneric or conspecific competitors (*post hoc* Tukey's tests, all $p > 0.05$). The only exception was that the outcome between congeners was not significantly different from that between suborders (*post hoc* Tukey's test, $T = -3.05$, $p = 0.052$). There was also a significant change in the proportion of competitors showing mutual aggression with increasing taxonomic relatedness in Antarctic bryozoans (ANOVA, d.f. = 7,164, $F = 21.3$, $p < 0.001$). The trend of increasing mutual aggression with increasing taxonomic difference bore some resemblance to that of increasing displacement with increasing taxonomic divergence, and was robust to both taxa and environment.

The proportion of confamilial species that showed mutual aggression was more than three times that of conspecifics, whilst the equivalent value for congeneric species was more than double that for conspecifics. The trend of decreased aggression with increased relatedness was simi-

lar in bryozoans from two different environments and in a distantly related group (ascidians), and therefore appears to be highly robust to environment and organism identity (phylum), within these data, at least. The underlying suggestion by Darwin (1859) (echoed by later authors, for example Woodin & Jackson (1979)) was that competition would be more intense between more closely related competitors. The results here do not completely support Darwin's suggestion but they do fit with the first hypothesis of Diamond (1987).

4. DISCUSSION

The outcomes, effect and even prevalence of competition have been contentious issues in ecology for more than a hundred years. A dichotomy in viewpoints developed among ecologists seeking to explain why laboratory experiments demonstrated competitive displacement of species (leading to extinction) while this was not apparent in the field. These polarized ideas assumed either that competition rarely occurred or that, conversely, it was so frequent that intensive adaptation of, and partitioning by, competitors minimized its effects. There are places and resources, however, in which direct (interference) competition can easily be seen and measured, for example living space (which controls access to food and mates) on rocky (coastal) intertidal and subtidal zones (figure 1). Although much of the pioneering work on competition investigated food partitioning in birds, battles for space, particularly by plants, became recognized as an important testing ground for the many problems and paradoxes surrounding concepts in competition. Space is an unusual resource, one for which even members of different kingdoms (Hochberg & Lawton 1990) are in frequent competition. The work of Connell (1961a,b) on competition between coastal taxa (barnacles) was one of the early and important demonstrations of the mechanisms involved. Nearly all the many studies of coastal competition that have followed, like Connell's work, have focused on closely related taxa, although many different types of animal have now been studied. The science that led to the hypotheses of Diamond (1987) (see Brown & Davidson 1979; Levins 1979; May *et al.* 1979; Schluter 1986) demonstrated that even very distantly related animals could be strong competitors, and the results were very asymmetric. All of these studies involved competition between phyla (vertebrates versus various invertebrates) although Furness (1982) and Hurlbert *et al.* (1986) suggested strong competition for food between different classes of vertebrates. Ecological research, for more than a hundred years after Darwin (1859), had still shown only that competitors for a common resource could be closely or very distantly related and that there were levels of asymmetry at each end of the taxonomic spectrum.

Strongly asymmetrical outcomes of competition between man and other species (such as seabirds for fish; Furness 1982) are obvious, but the data presented here show outcome asymmetry does not vary continuously with competitor relatedness. The test of the core hypothesis of the present study, the second prediction of Diamond (1987), did find increasing asymmetry of competitor displacement with increasing taxonomic divergence in the data tested here, but with a complication. A simple

Figure 1. Spatial interference competition between various taxa (mainly bryozoans) in Antarctic shallow-water rocks. Interactions include conspecific: *Celleporella antarctica* (1); congeneric: *C. antarctica* versus *C. bougainvillei* (2); within-suborder: *C. antarctica* versus *Inversiula nutrix* (3); within-order: *C. antarctica* versus *Beania erecta* (4); within-phylum: *Microporella brevissima* versus *Patinella* sp. (5); within-kingdom: *B. erecta* versus unknown demosponge (6); and between-kingdom: *C. antarctica* versus calcareous algae *Lithothamnion* sp. (7). Insert shows detail of mutual aggression between colonies.

Figure 2. The relationship between competitor relatedness and the probability of showing competitor displacement in interference competition. Data are presented as (a) original values for bryozoans in intrakingdom through to intraspecific competition and (b) means with standard error. *x*-axes are (a) categorical or (b) shown scaled according to Nei's genetic identity. All regressions shown were conducted on raw data (shown as means for clarity of trend) and are significantly different from zero (ANOVA, d.f. = 1,103, $F = 102.2$ and d.f. = 1,53, $F = 70.4$, both $p < 0.001$, for bryozoans ($y = 0.775 - 0.619x$, $r^2 = 0.493$) and ascidians ($y = 0.593 - 0.445x$, $r^2 = 0.563$), respectively). (b) Family, genera and species data are shown as mean $\pm$ s.e. ($n = 15$ for each taxonomic division). Key: bryozoans (temperate), filled circles; bryozoans (Antarctic), open circles; ascidians (temperate), squares.

Figure 3. Relationship between competitor relatedness and probability of showing mutual aggression in interference competition. Data presentation, x -axes and symbols are as in figure 2. (b) Regression shown was conducted on raw data (shown as means for clarity of trend) and is significantly different from zero (ANOVA, d.f. = 1,156, $F = 161.3$, $p < 0.001$). The regression equation and fit are $y = 0.855 - 0.707x$, $r^2 = 0.505$.

relationship occurred between competitor relatedness and asymmetry of competition outcome from conspecific to confamilial levels of relatedness. Typical (mean) probabilities of consistent displacement in encounters between congeners were, therefore, where they would be predicted by mean genetic similarity from Nei's genetic index. The complication was that competition asymmetry was not significantly different between same-superfamily and same-kingdom competitors. Diamond's second prediction may have been accepted, but the comments of Darwin (1859) were subtly different.

Was the underlying suggestion of Darwin (1859), that competition would be more intense between more closely related competitors, right? To answer this question requires evidence from the results of both the hypotheses tested here because they conflict. Based on the evidence of outcome asymmetry (figure 2) alone I would argue that he was correct. The results presented here demonstrate that more closely related bryozoans and ascidians were more evenly matched in competitive encounters, which would suggest longer harder battles. However, more closely related competitors also showed reduced levels of mutual aggression (figure 3), which clearly contradict any concept of increased intensity. Why mutual aggression declines with increasing competitor genetic similarity is unclear as overgrowth by any competitor, irrespective of relatedness, can be fatal. A possible explanation could, nevertheless, be linked to the consequences of spatial battles. As contests between closely related competitors often result in tied outcomes, it would seem intuitively reasonable that selection might favour individuals that conserve effort and fight only those of most importance.

The results obtained here would suggest that, as the consequences of fights with more distantly related competitors result more often in overgrowth, these are the more important contests. When organisms compete for mates, or space to access mates, however, only intraspecific contests are important. Although both hypotheses of Diamond (1987) have been supported, the complexity behind the suggestion of Darwin (1859) that led to these hypotheses makes it difficult to demonstrate them categorically as right or wrong.

The evidence that the bryozoans from two very different regions (temperate Europe and the outlying Antarctic islands) and a distant group of animals, the ascidians, all showed a similar trend suggests the relationship to be robust. Testing this with other organism datasets may not, however, be easy; there are few taxa that both have many subdivisions at all levels and compete for a similar resource. Bryozoans have proved a particularly suitable taxon for unravelling the relationships between competition and relatedness (this study), behaviour (Grosberg 1981) and wide-scale patterns in space (Barnes 2002) and time (McKinney 1995; Barnes & Dick 2000). Corals are also an obvious taxon that may meet both requirements and for which some competition data exist (e.g. Chornesky 1989).

The implications of the present findings on competitive displacement stretch from genetics to interpretations of historical clade displacement (e.g. McKinney 1995; McKinney *et al.* 1998; Barnes & Dick 2000). Many studies of competition conclude that competitor identity is an overriding factor influencing outcome. The findings here may help explain why this is the case: outcome asymmetry

doubles between congenerics and trebles between confamilials relative to conspecifics. The outcomes of competition seem to be equally asymmetric between bryozoan or ascidian competitors of different families and directly between a bryozoan and an ascidian despite (to us) the apparent difference in morphological divergences. Looks are clearly not everything in the battle for space. Whilst the hypothesis of Jackson (1979), that competition between different types of organism (phyla) should result in more extreme outcomes than that between organisms of common structure (such as bryozoans), seemed intuitively reasonable, the data presented here suggest otherwise. Bryozoan data given here show that outcomes of competition are equally asymmetric between competitors of the same superfamily and between those of different phyla. Most recognizable organism types (phyla) were distinct in the Cambrian (*ca.* 570 Myr ago) while new families emerge in just tens of millions of years, but this is enough, it seems, to make organisms sufficiently distinct for an unfair fight.

The author thanks Professor Andrew Clarke, Professor Lloyd Peck and two anonymous referees for their highly constructive comments leading to a greatly improved manuscript.

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