

Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae

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Although many studies have investigated how community characteristics such as diversity and disturbance relate to invasibility, the mechanisms underlying biotic resistance to introduced species are not well understood. I manipulated the functional group composition of native algal communities and invaded them with the introduced, Japanese seaweed *Sargassum muticum* to understand how individual functional groups contributed to overall invasion resistance. The results suggested that space preemption by crustose and turfing algae inhibited *S. muticum* recruitment and that light preemption by canopy and understory algae reduced *S. muticum* survivorship. However, other mechanisms I did not investigate could have contributed to these two results. In this marine community the sequential preemption of key resources by different functional groups in different stages of the invasion generated resistance to invasion by *S. muticum*. Rather than acting collectively on a single resource the functional groups in this system were important for preempting either space or light, but not both resources. My experiment has important implications for diversity–invasibility studies, which typically look for an effect of diversity on individual resources. Overall invasion resistance will be due to the additive effects of individual functional groups (or species) summed over an invader's life cycle. Therefore, the cumulative effect of multiple functional groups (or species) acting on multiple resources is an alternative mechanism that could generate negative relationships between diversity and invasibility in a variety of biological systems.

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One generality that has emerged from studies of invasive species in a wide variety of systems is that disturbed communities are more easily invaded (Elton 1958, Hobbs and Huenneke 1992, Burke and Grime 1996, Kotanen 1997, Rachich and Reader 1999). In sum, this work suggests that intact native communities are capable of exerting considerable resistance to non-indigenous species, but the mechanisms underlying this resistance are usually unclear. In theory, disturbance facilitates invasions because it increases resource availability and decreases competition from native species (Elton 1958,

Prieur-Richard and Lavorel 2000). Although several empirical studies in terrestrial grasslands have demonstrated that resource preemption by native species generates invasion resistance (Naeem et al. 2000, Prieur-Richard et al. 2000, Dukes 2001, Seabloom et al. 2003), the mechanistic basis of resistance has rarely been investigated in other biological systems and the generality of this mechanism is therefore uncertain. In the present study, I used a field experiment to examine the mechanisms underlying invasion resistance in a community of benthic marine algae.

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The introduced Japanese seaweed *Sargassum muticum* has been invading nearshore marine communities in Washington State since its accidental introduction in the early 20th century (Scagel 1956). Shallow, subtidal habitats in this region are dominated by algae, which form a species rich and structurally complex community. This algal community has three distinct functional components (layers): a canopy of large brown algae, an understory of fleshy red algae, and a bottom layer of encrusting and turf-forming red algae. Each of these functional groups has the potential to influence the other two and interactions among these three groups can have important consequences for local community structure (Kennelly 1987, Clark et al. 2004). For example, canopy and understory algae compete for light (Pearse and Hines 1979, Dayton et al. 1984, Clark et al. 2004) and frond sweeping by these relatively large macroalgae can negatively influence species growing beneath them (Black 1974, Vadas et al. 1992, Leonard 1999, Connell 2003). Likewise, crustose and turfing algae can reduce the postsettlement survivorship of other species by tissue sloughing (Johnson and Mann 1986, Keats et al. 1997) and enhancing sedimentation rates (Isaacs et al. 2004). In this system light and space are particularly important limiting resources and these three groups of algae differ in the way they use those resources. Canopy and understory algae take up relatively little primary space on the substratum but they can have strong effects on light availability (Pearse and Hines 1979, Dayton et al. 1984). In contrast, encrusting and turf-forming algae occupy most of the primary space, but are extremely shade tolerant (Airoldi 2000) and therefore require very little light.

I was interested in understanding the role that each of these algal groups played in resisting invasion by *S. muticum*. I predicted that different resources were likely to be limiting *S. muticum* in different stages of the invasion. In order to test this prediction I experimentally invaded communities of native algae with the introduced Japanese seaweed *Sargassum muticum*. By manipulating the presence of particular functional groups and assessing invader performance during each phase of the subsequent experimental invasion, I hoped to elucidate the role that different native functional groups played in resisting invasion by *S. muticum*. Specifically, I was interested in whether the identity of functional groups that were important for invasion resistance changed as the invasion progressed, and whether that change was related to the preemption of key resources required by *S. muticum* during different stages in its life cycle. This study is one of the first to investigate the mechanistic basis of invasion resistance in a marine community and it is the first to do so in a community of marine algae. Because I manipulated natural algal communities in the field and examined both pre- and post-settlement phases of the invasion process my results yielded important insights into how communities resist invasion.

Material and methods

Study site

This research was based out of Friday Harbor Laboratories on San Juan Island, Washington State, USA. Field work was accomplished using SCUBA in shallow subtidal kelp communities. The field experiment was carried out from May, 2001 to April, 2002 at a site within the San Juan Islands Marine Preserve network adjacent to San Juan Island, known locally as Fern Point (48° 33.602'N, 123°00.761'W). These reserves were established in 1990 and are closed to harvesting with very limited exceptions (e.g. salmon).

Native functional groups

I divided the species within the native algal community into three functional groups based on similarities in morphology and resource use (Littler 1980, Steneck and Watling 1982, Dayton et al. 1984, Dayton 1985, Steneck and Dethier 1994; see Gabrielson et al. 2000 for species authorities): 1) the canopy functional group contains large, brown algae (Phaeophyceae: *Agarum fimbriatum*, *Agarum clathratum*, *Laminaria bongardiana*, *Laminaria complanata*, *Costaria costata* and *Desmarestia ligulata*) that occupy relatively little primary space but have large blades that allow them to effectively exploit light, 2) the understory functional group contains smaller, fleshy algae (Rhodophyta: *Chondracanthus exasperatus*, *Odonthalia* spp., *Laurencia spectabilis*, *Plocamium cartilagineum*, *Rhodoptilum plumosum*, *Polyneura latissima*, *Constantinea simplex*, *Mazzaella* spp., *Callophyllis* spp., *Cryptopleura ruprechtiana*, *Opuntia californica* and *Sarcodiotheca gaudichaudii*; Chlorophyta: *Ulva-Monostroma* spp.) that generally occupy little primary space and generally have less effect on light than canopy species due to their relatively small size, 3) the crust/turf functional group consists of encrusting (Rhodophyta: *Hildenbrandia occidentalis*, *Lithothamnion* spp. and *Lithophyllum* spp.) and filamentous, turf-forming algae (Rhodophyta, species unknown) that are the predominant space occupiers in this system but these species can only shade other algae by actually overgrowing them. These functional groupings were used because I expected the species within them to be functionally equivalent with respect to the questions in which I was interested.

The invader

Sargassum muticum is a brown alga in the order Fucales that is native to southeast Asia (Yendo 1907) and was introduced to Washington State in the early 20th century, probably with shipments of Japanese oysters that were imported for aquaculture beginning in 1902

(Scagel 1956). It is a common species in shallow subtidal habitats throughout Puget Sound and the San Juan Islands, including marine preserve areas, and reaches densities as high as 126 individuals m^{-2} (Britton-Simmons, unpubl.). Because it grows several meters taller than most native algae, *S. muticum* reduces light availability and decreases the abundance of native algae (Britton-Simmons 2004).

Sargassum muticum has a simple life cycle. Reproductive structures called receptacles are borne along secondary branches and contain both oogonia and antheridia. After eggs are released from the oogonia they adhere to the external surface of the receptacle where they are fertilized. Fertilized embryos remain attached to the receptacle until they develop tiny, adhesive rhizoids, at which point they detach and recruit to the substratum in close proximity to the parent plant (Deysher and Norton 1982).

Field experiment

This experiment was designed to test the importance of canopy, understory and crust/turf functional groups for resisting invasion by *S. muticum*. The experiment had five treatments: 1) unmanipulated control, 2) canopy removal, 3) understory removal, 4) crust/turf removal, 5) all algae removal. This design allowed me to test the importance of each functional group individually in addition to looking for an interaction between the three groups. Each treatment was replicated seven times and the treatments were maintained every six weeks with the exception of the crust/turf removal treatment, which could not be maintained without affecting the juvenile *S. muticum* that had settled in the plots.

I selected 30×30 cm plots at a depth of -3 m MLLW that were comparable in biotic and abiotic characteristics and separated by a minimum distance of 1 m. After the plots were selected, I assigned them to treatments using a randomized block design. Specifically, the plots were divided into seven blocks of five adjacent plots and plots within each block were randomly assigned to treatments so that each block contained one replicate of each treatment. Canopy and understory algae were removed from the substratum by prying their holdfasts off the rock with a dive knife. The blades of canopy algae adjacent to plots in the canopy removal treatment were trimmed to prevent them from hanging over or abrading those plots. Crustose and turfy algae were removed using wire brushes, scraping implements and hammers. After imposing the experimental treatments I surveyed the plots to quantify the amount of bare rock in each plot and these data were then used in the subsequent statistical analyses to test the relationship between available space and *S. muticum* recruitment. None of the experimental plots contained *S. muticum* prior to the

experiment. However, some *S. muticum* was present at the site in the surrounding area and it was removed in June, 2001 (prior to reproduction) in order to prevent contamination of the experimental plots from external sources of *S. muticum* propagules.

The experimental plots were invaded by *S. muticum* immediately after treatments were imposed in August 2001. The experimental invasion was accomplished by collecting *S. muticum* from the field and transporting them to the lab where 300 g of reproductive *S. muticum* was placed in each 30×30 cm vexas bag. These bags were then returned to the field the same day and suspended over experimental plots for one week. The bags were held in place by cable ties attached to eyescrews that had been inserted into the rock substratum on either side of the plots.

I quantified *S. muticum* recruitment by counting the number of *S. muticum* juveniles that were present in the plots 4 months after the experimental invasion (December 2001), when they first became visible in the field. Survivorship was assessed by measuring the number of *S. muticum* individuals that survived from December 2001 to April 2002.

Light measurements were taken in all plots in the crust/turf removal and all algae removal treatments on a clear, sunny day in July, 2002 using a Li-cor LI-1000 Data Logger (Li-Cor Biosciences, Lincoln, NE, USA) coupled to two quantum irradiance sensors. One sensor was kept at the surface in a boat while the other was deployed underwater to take readings in each experimental plot at a depth of 4 m. The underwater sensor was placed in the center of each plot at a height of 12 cm above the substratum (the lowest position possible with this equipment) and measurements were taken simultaneously at the surface and at depth so that percent transmittance could be calculated for each plot. I used the average of 60 instantaneous measurements taken at one second intervals as the datum for each plot.

Results

The *Sargassum muticum* recruitment data were analyzed using ANOVA with treatment and block as main effects, followed by a series of planned comparisons to test 4 specific a priori hypotheses I had about the role of different groups of native species in resisting invasion by *S. muticum* (Table 1). In the ANOVA analysis, the experimental treatments explained a significant amount of variation in *S. muticum* recruitment ($F_4 = 10.50$, $P < 10^{-4}$, Fig. 1). Because my planned comparisons were not orthogonal to each other I used the sequential Bonferroni method to adjust the critical significance value (Sokal and Rohlf 1995). The planned comparisons showed that removing canopy and understory algae did not cause a significant increase in

Table 1. Summary of planned comparisons testing a priori hypotheses about the role of native functional groups in resisting recruitment by *S. muticum*. Treatment codes: 1 = control, 2 = canopy removal, 3 = understory removal, 4 = crust/turf removal, 5 = all algae removal.

Hypothesis	Test	F ratio	P
Canopy algae reduce recruitment by <i>S. muticum</i>	1 vs 2	0.157	0.696
Understory algae reduce recruitment by <i>S. muticum</i>	1 vs 3	1.293	0.267
Crustose and turfy algae reduce recruitment by <i>S. muticum</i>	1 vs 4	16.501	0.000
Algal groups interact to reduce recruitment by <i>S. muticum</i>	(2+3+4) vs 5	0.065	0.802

S. muticum recruitment ($P > 0.25$ in each case, Table 1, Fig. 1). However, removal of crustose and turfy algae resulted in a significant increase in *S. muticum* recruitment ($P < 0.001$, Table 1, Fig. 1). Finally, there was no evidence that the three groups of algae interacted to reduce recruitment by *S. muticum* ($P = 0.802$, Table 1, Fig. 1).

When I combined the recruitment data across all treatments and regressed the number of *S. muticum* recruits (square root transformed) on the percent cover of bare rock after the experimental treatments were imposed, the relationship was significant ($F_{1,33} = 27.80$, $P < 10^{-5}$, Fig. 2). This result suggests that space was the resource limiting *S. muticum* recruitment.

Only two treatments (crust/turf removal and all algae removal, Fig. 1) had substantial numbers of *S. muticum* recruits and I therefore limited my analysis of post-settlement survivorship to those two treatments. The only difference between the two treatments was that canopy and understory algae were present in the crust/turf removal treatment and absent in the all algae removal treatment. The lack of variation in survivorship in the crust/turf removal treatment (Fig. 3) precluded the use of parametric statistics. Instead, I used a contingency test to ask whether the presence of *S. muticum* in experimental plots on the final sample date (April 2002) was independent of treatment. Those data showed that six out of seven plots in the all algae removal treatment still contained *S. muticum* but that none of the plots in the crust/turf removal treatment contained *S. muticum*. The contingency test results indicated that the survivorship of *S. muticum* was not independent of

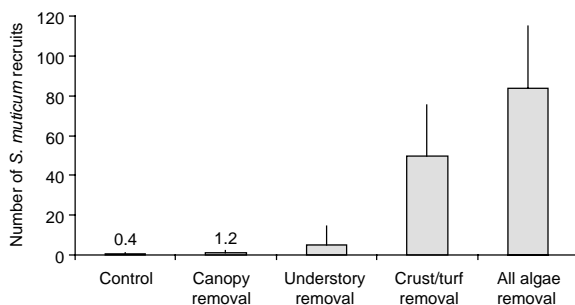


Fig. 1. Number of *S. muticum* recruits per plot (900 cm²). Means are given for control and canopy removal treatments. Error bars are +1 SE ($n = 7$).

treatment ($G = 5.02$, $P < 0.05$), suggesting that the presence of canopy and understory algae reduced the survivorship of *S. muticum* once it had recruited.

Analysis of the light data indicated that the transmittance of photosynthetically active radiation (PAR) was significantly lower in the crust/turf removal treatment compared to the all algae removal treatment (data were arcsin transformed, $t = 4.60$, $P < 0.001$, Fig. 4). This difference suggests that shading by understory and canopy algae was the mechanism that decreased *S. muticum* survivorship in the crust/turf removal treatment. The lack of variation in survivorship data in the crust/turf removal treatment prevented further analyses to determine whether canopy, understory or both groups of algae were responsible for the survivorship effect I found.

Discussion

In this community of marine algae resistance to invasion arose due to the sequential preemption of key resources by different native functional groups in different stages of the invasion (Fig. 5). In the initial stage of the

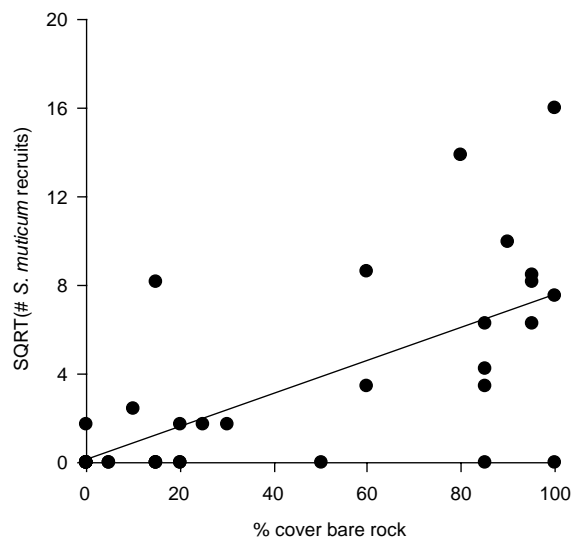


Fig. 2. Relationship between the number of *S. muticum* recruits and bare space available on the rock substrate after the experimental treatments were imposed ($R^2 = 0.46$, $P < 10^{-5}$).

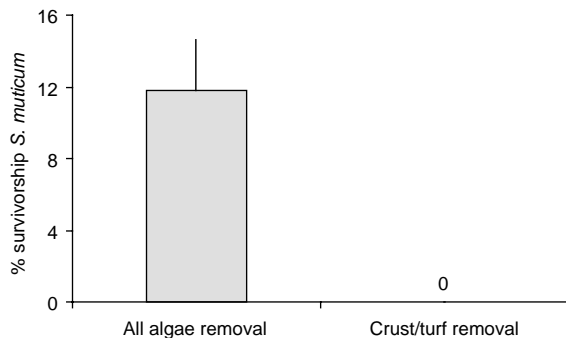


Fig. 3. Percent survivorship of *S. muticum* from 4 to 8 months of age. No *S. muticum* recruits survived in the crust/turf removal treatment. Error bars are +1 SE (n = 7).

invasion, crustose and turfy algae inhibited successful recruitment by *S. muticum*. My data suggest that this occurred because the species in this functional group reduced the availability of space. However, mechanisms other than space preemption may have contributed to the recruitment inhibition effect. For example, sloughing of epithelial layers by crusts (Johnson and Mann 1986, Keats et al. 1997) and high rates of sedimentation in turfs (Isaews et al. 2004) could have reduced the survivorship of the early post-settlement phase of *S. muticum*, thereby reducing the number of individuals I counted as recruits. In contrast to the strong effects of crustose and turfy algae, canopy and understory algae did not significantly reduce *S. muticum* recruitment.

Despite their lack of importance in the initial invasion stage, canopy and understory algae reduced the survivorship of *S. muticum* once it had recruited into the community. The reduced survivorship of *S. muticum* in plots where canopy and understory algae were present was associated with significantly reduced light levels in this treatment, suggesting that shading was the mechanism. Nevertheless, additional factors such as frond sweeping (Black 1974, Vadas et al. 1992, Leonard 1999, Connell 2003) and sedimentation (Eckman et al. 1989, Airolidi and Cinelli 1997) may have contributed to the survivorship effect. These results collectively demon-

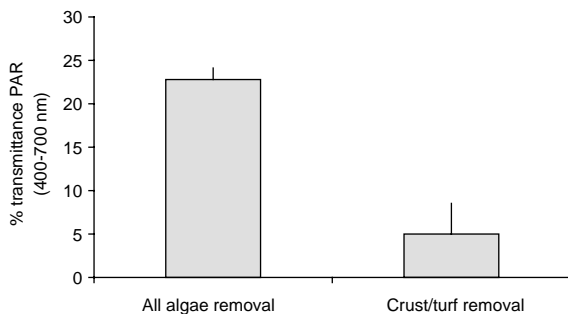


Fig. 4. Percent transmittance of photosynthetically active radiation (PAR, 400–700 nm wavelengths). Error bars are +1 SE (n = 7).

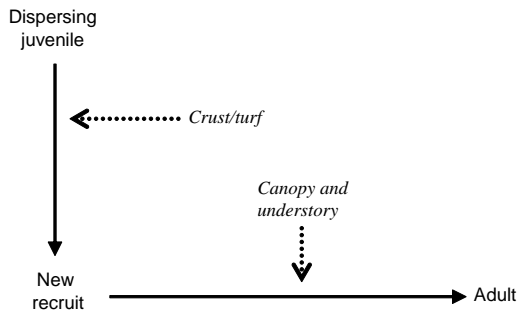


Fig. 5. Schematic diagram of the invasion process indicating the phases in which different native functional groups were important for resisting the *S. muticum* invasion.

strate that the native functional groups important for resistance changed as the invasion progressed (Fig. 5). This occurred because the resource limiting the *S. muticum* invasion varied through time.

Why weren't canopy algae important for inhibiting *S. muticum* recruitment? Many canopy algae have large holdfasts, which cover a substantial area of rock, and in theory they should have been important for resisting *S. muticum* recruitment if space was the limiting resource. Indeed, a previous study in California found that removing canopy algae increased *S. muticum* recruitment (Deysher and Norton 1982). However, in this system, as in others (Airolidi 2000), removing canopy algae rarely creates available space because there is usually a layer of crustose algae under their holdfasts (Britton-Simmons, pers. obs.). These crustose algae are slow growing species that are capable of surviving overgrowth by other species for considerable periods of time (Airolidi 2000, Dethier and Steneck 2001). Thus, canopy algae were probably unimportant for resisting *S. muticum* recruitment because they were functionally redundant in terms of space preemption.

It would be interesting to know the proportional contribution that understory and canopy algae each made to the survivorship effect. The results of this experiment did not allow me to separate out the effect of each of these two groups, and it is possible that only one of them reduced *S. muticum* survivorship. However, understory (Chapman 1984, Dayton et al. 1984) and canopy (Pearse and Hines 1979, Johnson and Mann 1988) algae are both known to shade algae growing beneath them, and it is likely that both groups of algae contributed to the overall effect.

Undisturbed algal communities in this system that contain all functional components appear to be highly resistant to invasion. Nevertheless, *Sargassum muticum* is common in shallow, subtidal habitats throughout the San Juan Islands. How is this possible? My experiment suggests that patches which lack one or more native functional groups will be more vulnerable to invasion. When selecting experimental plots for this study I purposely chose areas where all three functional groups

of algae were present. In reality, however, grazing by herbivores makes these subtidal communities a mosaic of patches that vary in terms of which functional groups are present (Vadas 1968, Duggins 1983, Britton-Simmons, pers. obs.). For example, the large chiton *Cryptochiton stelleri* feeds selectively on understory red algae and the green urchin *Strongylocentrotus droebachiensis* feeds on a variety of algae, creating bare space which can then be utilized by native and non-native species alike. This study demonstrates that this natural variation in functional group composition has important implications for the ability of these communities to resist invasion.

Only three other experimental invasion studies testing the role of native functional groups have also measured resource availability, and they were all carried out in terrestrial systems. These experiments showed that the effect of functional group diversity on invasion success ranges from strong (Dukes 2001) to weak (Symstad 2000) to undetectable (Prieur-Richard et al. 2000). Only one of these studies (Dukes 2001) found strong evidence that functionally diverse communities reduced resource availability. However, all three previous studies (Prieur-Richard et al. 2000, Symstad 2000, Dukes 2001) showed that particular functional groups had strong effects on specific resources, and consequently those groups were important determinants of community invasibility. These studies and my own experiment all provide evidence that individual functional groups can be important for invasion resistance. Nevertheless, overall resistance will be due the additive effects of all functional groups summed over the invader's entire life cycle. Strong effects of particular functional groups at different stages of the invasion, as was the case in my system, could therefore generate a negative relationship between functional group diversity and invasibility, even if there is not a negative relationship between diversity and the availability of any single resource. In systems where this is the underlying cause of a negative relationship between diversity and invasibility it will be important to determine how each functional group contributes to resistance in order to understand the overall pattern.

This experiment highlights several important methodological issues that should be taken into consideration in designing future experiments to examine the biotic resistance phenomenon. First, my study demonstrates that each phase of the life cycle may yield incremental insights into the overall process, and it is therefore advantageous to examine as much of the life cycle as possible (Lavorel et al. 1999). Second, this study and other recent examples (Stachowicz et al. 1999, Naem et al. 2000, Prieur-Richard et al. 2000, Dukes 2001, Dunstan and Johnson 2004) illustrate the importance of measuring resource availability in order to understand the mechanistic basis of experimental patterns. Third, utilizing natural communities ensures that important

community features (e.g. the redundant use of space by canopy algae), which may be absent from contrived communities but are important for understanding resistance, are left intact (Dunstan and Johnson 2004). Future studies that examine the entire life cycle of the invader, make use of natural communities, and measure resource availability should yield considerable insight into the mechanisms underlying invasion resistance.

Although resource preemption has been shown to generate invasion resistance in a number of terrestrial communities (Naem et al. 2000, Prieur-Richard et al. 2000, Symstad 2000, Dukes 2001, Cleland et al. 2004, Levine et al. 2004) there is scant evidence from other biological systems to support the generality of this mechanism. In combination with recent work in marine invertebrate communities (Stachowicz et al. 1999, 2002, Dunstan and Johnson 2004) this study suggests that resource preemption is also an important process underlying biotic resistance in marine systems. Rather than acting collectively on a single resource, native functional groups in this community reduced the levels of two different resources that were critical for *Sargassum muticum* recruitment and survival. Consequently, as the resource limiting the *S. muticum* invasion changed, so did the native functional group(s) that were important for resistance. The sequential preemption of key resources by different functional groups in different stages of the invasion may be a general mechanism underlying negative relationships between diversity and invasibility in a variety of systems.

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