The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos

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Abstract

The intermediate disturbance hypothesis is a widely accepted generalization regarding patterns of species diversity, but may not hold true where fire is the disturbance. In the Mediterranean-climate shrublands of South Africa, called *fynbos*, fire is the most importance disturbance and a controlling factor in community dynamics. The intermediate disturbance hypothesis states that diversity will be highest at sites that have had an intermediate frequency of disturbance and will be lower at sites that have experienced very high or very low disturbance frequencies. Measures of diversity are sensitive to scale; therefore, we compared species richness for three fire regimes in South African mountain fynbos to test the intermediate disturbance hypothesis over different spatial scales from 1 m^2 to 0.1 hectares. Species diversity response to fire frequency was highly scale-dependent, but the relationship between species diversity and disturbance frequency was opposite that predicted by the intermediate disturbance hypothesis. At the largest spatial scales, species diversity was highest at the least frequently burned sites (40 years between fires) and lowest at the sites of moderate (15 to 26 years between fires) and high fire frequency (alternating four and six year fire cycle). Community heterogeneity, measured both as the slope of the species-area curve for a site and as the mean dissimilarity in species composition among subplots within a site, correlated with species diversity at the largest spatial scales. Community heterogeneity was highest at the least frequently burned sites and lowest at the sites that experienced an intermediate fire frequency.

Introduction

Species diversity is a topic that has long intrigued biologists and has yet eluded general explanations. Mediterranean-type climate shrublands are notably diverse among temperate regions: a striking example is the Cape Floristic Region of South Africa which has one of the highest plant species densities of any temperate region and remarkable levels of endemism (Cowling et al. 1992). The intermediate disturbance hypothesis (Connell 1978; Huston 1979) states that diversity will be highest at sites that have had an intermediate frequency of disturbance that prevents competitive exclusion and will be lower at sites that have experienced very high or very low disturbance frequencies. Fire is a common disturbance yet little research

has attempted to quantify the effect of fire frequency on species richness. Support for the intermediate disturbance hypothesis has come primarily from studies of sessile marine organisms (Sousa 1984). There is little support for the intermediate disturbance hypothesis in fire-prone communities. Studies in Scottish heathlands have shown a simple increase in diversity with increasing fire frequency (Hobbs et al. 1984) and one of the few studies specifically of fire frequency and diversity (Collins 1992) suggested that the intermediate disturbance hypothesis may not hold true in North American grasslands where fire is the disturbance.

Temporal changes in species richness following fire can complicate investigation into the effect of fire frequency on species diversity. In South African fynbos, species richness peaks in the first year

after fire and then declines as the community ages (Kruger 1983; Hoffman et al. 1987; Le Maitre 1987; Cowling & Gxaba 1990). Other Mediterranean-climate shrublands, including California chaparral, also exhibit marked temporal variation in species diversity following fire primarily as a result of the diverse post-fire herbaceous flora (Keeley et al. 1981). Any study of fire frequency and diversity in fire-prone shrublands must avoid confounding such diversity patterns within a fire cycle with changes caused by variation in the length of each cycle. Diversity should be compared among sites at the same stage in post-fire succession.

Another problem in investigating species diversity is the extreme scale dependence of measures of diversity. Conclusions regarding species diversity are dependent upon the scale examined. For example, it is possible for one of two sites to be more diverse at a point scale of 1 m^2, while the other site may have more species in 0.1 hectare because of greater 'turnover'. Although one site had a large number of species in a very small area, fewer species were added as sampling size increased. This turnover within a community has been called 'internal beta diversity', 'pattern diversity' (Whittaker 1977; Magurran 1988), or 'community heterogeneity' (Collins 1992). The intermediate disturbance hypothesis makes no prediction regarding the effect of disturbance frequency on community heterogeneity.

Disturbance is an important mechanism for producing spatial heterogeneity (Collins 1989, 1992; Chaneton & Facelli 1991). In the Mediterranean-climate shrublands of South Africa, called *fynbos*, fire is the most importance disturbance and may be a controlling factor in patterns of species richness. An assessment of community heterogeneity attempts to describe the interaction of scale and species richness, to measure the patchiness of species distributions. Heterogeneity can be measured in a variety of ways. The most intuitive representation of heterogeneity is the slope of a species-area curve constructed by sampling nested plots (Whittaker 1977; Bond 1983; Shmida 1984). Collins (1992), however, measured community heterogeneity as the mean degree of dissimilarity in species composition among multiple points in a community. Both methods attempt to include the effects of scale in describing community diversity.

In this study, we compared species richness for three fire regimes in South African mountain fynbos to test the intermediate disturbance hypothesis over different spatial scales from 1 m^2 to 0.1 hectares. We then investigated the effect of fire frequency on community

heterogeneity. A nested plot sample design allowed measurement of heterogeneity by constructing species-area curves and by calculating point to point mean difference in species composition. By selecting nearly even-aged sites, we attempted to isolate the effect of fire frequency from the effects of stand age since the last fire.

Materials and methods

Study area

This study was conducted in the Jonkershoek Valley, Hottentot's Holland Nature Reserve, about 15 km east of the town of Stellenbosch, Western Cape Province, South Africa. The area lies at 33°57′ S and 18°55′ E and is within the Mediterranean-climate region of South Africa characterized by cool, wet winters and hot, dry summers (Versfeld et al. 1992). Areas of the valley have been burnt under a variety of different fire regimes for research and as a part of the normal management of fynbos water catchments (van Wilgen & McDonald 1992). All study sites had a north-facing (equatorial) aspect and were at approximately 320 m elevation. Mean annual rainfall measured at 305 m near the study sites was 1523 mm (Versfeld et al. 1992). Sites were on acid, quartzite-derived soils.

Three areas of the north-facing slopes of Jonkershoek valley that had experienced different fire frequencies were selected for study. The high fire frequency sites were last burned in a control-burn on 17 March 1987; previously, the area was burned on an alternating four and six year fire cycle. Directly adjacent were the intermediate fire frequency sites that last burned in the same March 1987 fire. Previous recorded fires at the intermediate frequency sites occurred in 1927, December 1942, and February 1958 (van Wilgen & McDonald 1992). The low fire frequency sites were less than a kilometer away and last burned in 1942 and in 1989. The slope angle at all sites ranged from 20 ° to 23 °. Mesic mountain fynbos communities comprised all these sites (McDonald 1985). The most obvious common shrubs at all sites were *Cliffortia cuneata*, *Protea neriifolia*, and *Protea repens*. *Erica hispidula* and members of the Restionaceae were common understory plants at all sites.

Although three fire frequency regimes cannot characterize the entire range of possible fire frequencies, the high and low fire frequency regimes here are known to lie at the extremes of fynbos fire frequencies for the
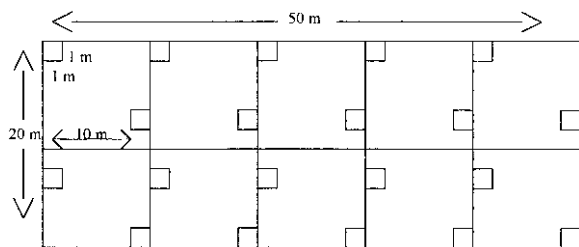
Figure 1. Modified 'Whittaker plot' used in constructing species area curves.

area. Fynbos doesn't accumulate enough fuel to burn at higher frequencies. The intermediate fire regime in this study approximates what has been considered a healthy fire frequency by fynbos managers.

Data collection

Each of the three disturbance regimes was represented by three sample sites. At each of the three areas, three 01. ha sites (20 m × 50 m) were laid out. The replicate sample plots were placed randomly within a fire regime area (between 50m and 600m apart) and were positioned to avoid gullies or rock outcrops and to include what was judged to be a single community. The sampling design was similar to the 'Whittaker plot' (Shmida 1984), but modified as described by Keeley et al. (1995) comprising of 10 non-overlapping 100 m^2 plots nested within a site. These plots each contained two 1 × 1 m subplots offset from opposite corners of the 10 × 10 m plot (Figure 1). Each 20 × 50 m site was laid out with the long axis parallel to the slope contour. Species lists for the 1 × 1 m subplots, the 10 × 10 m plots, and the 0.1 hectare sites were made during June and July 1995.

Data analysis

Species area curves were constructed for each site and for each fire regime. Scales in addition to the 1 m^2, 100 m^2, and 0.1 hectare were added to the curves by combining species lists of all 13 combinations of two adjacent 10 × 10 m sites for a scale of 200 m^2, all four combinations of four 10 × 10 m plots forming squares for a scale of 400 m^2, and both combinations of six 10 × 10 m plots forming 20 × 30 m rectangles for a scale of 600 m^2. The 400 and 600 m^2 plots were restricted to rectangular combinations so as to better approximate the shape of the 20 × 50 m site. Regression analysis was used to describe the species area curves at each

site and in each fire regime in both semi-log and in log-log space.

Statistical analysis and computation were carried out using Systat (Wilkinson 1990) and Biodiv 4.1 (Baev & Penev 1993). Mean species richness for each spatial scale was compared across all three fire regimes using Kruskal-Wallace and Mann-Whitney tests because parametric procedures were not justified with the meristic variable, species richness. To account for spatial dependence of subplots within a site, all statistical tests were based on the three replicate sites in each fire regime. For the smaller scales with multiple subplots per site, all richness values were averaged on a plot basis, then the three replicate plots in each regime were used to generate a mean and standard deviation. In unplanned pairwise Mann-Whitney tests, a Bonferroni-type adjustment was used to control the experiment-wide alpha level.

Heterogeneity was defined as the mean dissimilarity (D) between points in a community and was calculated for all 190 pairwise combinations of 1 × 1 m subplots within a site. Dissimilarity, which varies from 0.0 to 1.0, was defined as:

D = 1 − C_S,
C_S = 2a/(b + c),

C_S is the Czekanovski–Dice–Sorenson index recommended by Pielou (1972), Campbell (1978) and Magurran (1988); where a = the number of species in common to both sites, b = the number of species in one site and c = the number of species in the other. The 190 dissimilarity (heterogeneity) values in each replicate site were averaged, and the three averages were used to generate means and standard deviations for each fire regime. Analysis of variance was used to test differences in mean heterogeneity among the three fire regimes.

Results

Mean species richness was significantly different among the three fire regimes for the three smallest scales (Table 1). At all scales, the intermediate fire frequency regime had lower species richness than did the frequently burned sites (Figure 2). This difference was significant at the three smallest scales but not at the three largest scales (although all $P \leq 0.061$). The low fire frequency regime had the lowest mean species richness at 1 m^2, 9.5, but the highest mean species richness at 0.1 hectare, 86.7 (Figure 2). Although low fire frequency sites had significantly lower mean species

Table 1. Mean species richness, test statistics and probability values for the Kruskal–Wallace comparison of mean species richness at six spatial scales among three fire regimes.

Scale (m^2)	Fire Frequency	Mean Species Richness ± SD	Kruskal-Wallace test statistic (H)	Probability value (P)	Sample size (n)
1	High	16.6 ± .503	6.0	0.050	3
	Intermediate	11.0 ± 1.58			
	Low	9.5 ± 1.67			
100	High	42.6 ± 1.06	7.3	0.027	3
	Intermediate	31.1 ± 1.27			
	Low	38.0 ± 0.58			
200	High	54.0 ± 2.48	6.5	0.039	3
	Intermediate	39.2 ± 2.51			
	Low	50.9 ± 1.81			
400	High	66.1 ± 4.72	5.7	0.058	3
	Intermediate	48.3 ± 4.79			
	Low	63.5 ± 1.5			
600	High	72.7 ± 6.74	5.6	0.059	3
	Intermediate	54.0 ± 5.60			
	Low	72.9 ± 1.54			
1000	High	80.0 ± 8.72	5.6	0.061	3
	Intermediate	64.7 ± 6.66			
	Low	86.7 ± 1.53			

richness than did the high fire frequency sites for the 1 m², 100 m², and 200 m² scales (all $P < 0.05$), the difference was not significant at the larger scales.

For each fire regime, species-area curves showed higher rates of species addition at the larger scales than predicted by a semi-log linear relationship. Polynomial regression ($r^2 = 0.96$, 0.94, and 0.97; $F_s = 5956$, 3193, and 5807; all $v = 1$, 151; all $P < 0.001$) better described the curves for each fire regime than did linear equations of the semi-log curves ($r^2 = 0.91$, 0.88, and 0.91). Linear regression of log-log plots also well described the three species-area curves ($r^2 = 0.95$, 0.87, and 0.96; $F_s = 2833$, 962, and 3186; all $v = 1$, 151; all $P < 0.001$) (Figure 3). Slopes of the log-log species-area curves at each replicate site within all fire regime areas ranged from 0.221 to 0.349 (Table 2). Analysis of covariance revealed a nearly significant difference between the slope of the high fire frequency log-log species-area curve (0.225) and that of the low fire frequency curve (0.321) ($F_s = 4.862$; $v = 1$, 8; $P = 0.059$).

Mean dissimilarity between 1×1 m plots within a site differed significantly among fire regimes ($F_s = 6.75$; $v = 2$; $P = 0.029$). Bonferroni pairwise

Table 2. Slopes and intercepts of log-log species-area curves for each site. The curves constructed for each fire regime use the mean species richness values at each scale among all three sites at each fire regime. The straight line in log-log space has an equation in the form log $S = z$ log $A +$ log c where $S =$ species richness and $A =$ area.

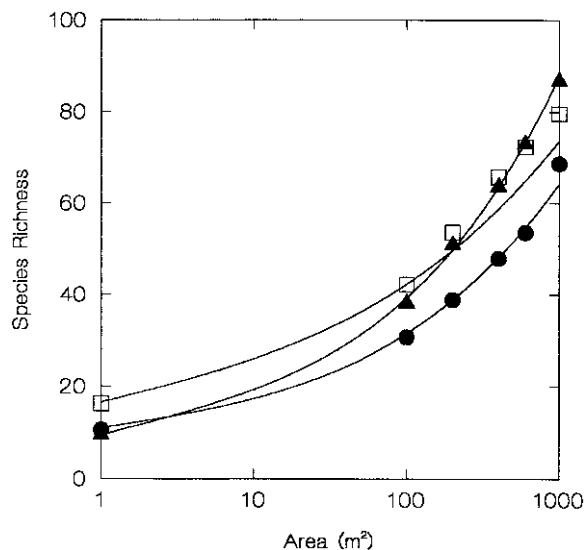| Site replicate	Slope (z)	Intercept (c)
1	0.229	1.221
2	0.221	1.197
3	0.224	1.213
High fire frequency regime (mean ± SD)	0.225 ± 0.004	1.210 ± 0.012
4	0.240	1.055
5	0.252	1.024
6	0.258	0.963
Intermediate fire frequency regime (mean ± SD)	0.250 ± 0.009	1.014 ± 0.047
7	0.349	0.895
8	0.324	0.941
9	0.289	1.042
Low fire frequency regime (mean ± SD)	0.321 ± 0.30	0.959 ± 0.75

Figure 2. Mean species richness and sample area for fynbos sites in the Jonkershoek Valley. Curves represent best fit lines from polynomial regression for each fire regime. Open squares are the high fire frequency sites (four and six year fire cycle); regression model richness = (log scale)$^{3.415}$ + 8.4 (log scale) +16.57 (r = 0.99, p < 0.001). Close circles are the intermediate fire frequency sites (29, 16, and 15 year fire cycle); regression model richnesss = (log scale)$^{3.292}$ + 5.34 (Log Scale) + 10.97 (r = 0.98, p < 0.001). Close triangles are the low fire frequency sites (42 years between fires); regression model richness = (log scale)$^{3.593}$ +8.87 (log scale) +9.423 (r = 0.991, p < 0.001).
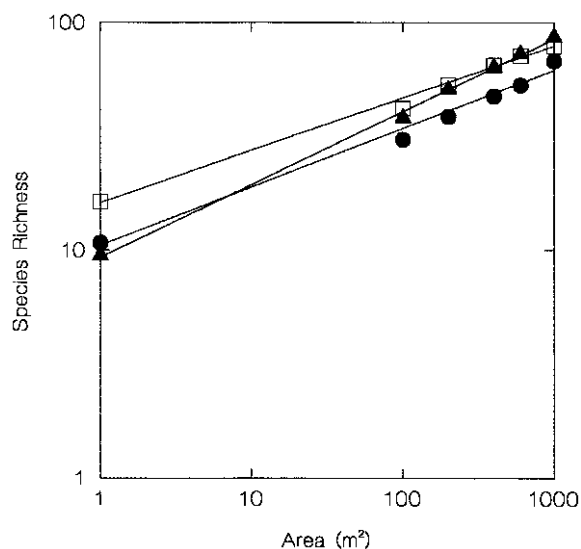

Figure 3. Mean species richness and sample area for fynbos sites in the Jonkershoek Valley. Same data as Figure 2 plotted in log–log space.

comparison showed that heterogeneity at the intermediate and low fire frequency regimes differed significantly (P = 0.033). Mean heterogeneity correlated exactly with mean species richness at the 0.1 hectare scale and was lowest (0.50) at the intermediate fire frequency and highest (0.64) at the low fire frequency sites (Figure 4).

Discussion

Despite a growing awareness of the importance of fire in many plant communities, few studies have investigated the role of fire frequency in creating patterns of species diversity. Although the intermediate disturbance hypothesis is a widely accepted explanation for patterns of species diversity at the alpha level, its support has come mainly from studies of marine intertidal organisms (Sousa 1984). The large spatial and temporal scales necessary for studies of fire frequency and diversity have made finding suitable sites very difficult and those few studies which have investigated the intermediate disturbance hypothesis in relation to fire (Collins 1989, 1992) have used grassland communities where fire is more easily managed than in shrublands. Although Collins (1992) suggested that the intermediate disturbance hypothesis may not hold true for North American grasslands, this study was weakened by confounding the pattern of diversity changes over time within a single fire cycle with the pattern produced by the frequency of such cycles. To avoid confounding these patterns, sites in the same stage of post-fire succession are required. The large spatial scales and the long time periods necessary to establish a fire history at a given site make problems of pseudo-replication unavoidable in an investigation of fire frequency and species diversity.

Although the intermediate disturbance hypothesis predicts that diversity will be highest at intermediate fire frequencies, the opposite was found in this study. Diversities at most spatial scales were lowest at sites that had experienced an intermediate fire frequency. Fire frequency had contrasting effects on species richness at different spatial scales: the least frequently burned sites had significantly lower species richness at 1 m^2, but the highest species richness at the larger scales. These different patterns at different spatial scales highlight the importance of examining heterogeneity as well as diversity. The heterogeneity results mirror the trend exhibited by the species richness pattern at the larger scales (Figure 4): sites that showed
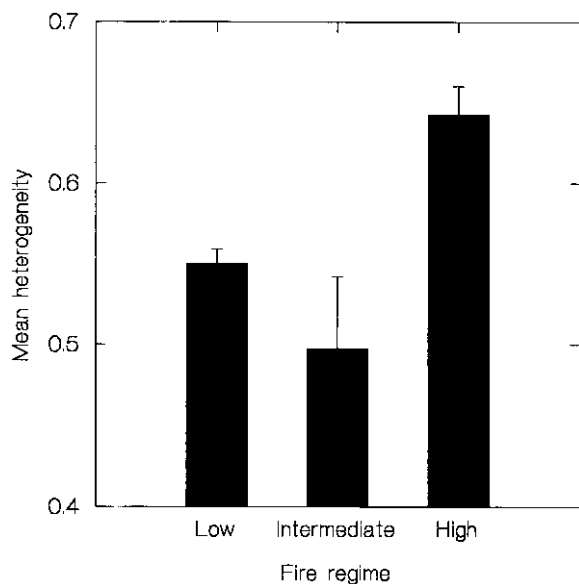
Figure 4. Mean heterogeneity by fire regime for sites in the Jonker-shoek Valley. Heterogeneity is defined as $1 - C_s$ where C_s is the Sorenson similarity coefficient calculated for all pairwise combinations of 1×1 m subplots within a site. The high fire frequency regime burned on an alternating four and six year fire cycle. The intermediate fire frequency regime burned at intervals of 15, 16 and 29 years. The low fire frequency regime experienced 42 years between fires. Error bars indicate one standard error.

a high degree of dissimilarity between 1 m² subplots were the most diverse at the 0.1 hectare scale. Fire frequency regimes were not replicated in this study as the site replicates for each regime all fell within a single burn. Therefore, it may be difficult to make generalizations from these results. Nevertheless, these patterns show a marked departure from the predictions of the intermediate disturbance hypothesis.

Mechanisms other than the competition invoked by the intermediate disturbance hypothesis may account for the patterns observed here. At the smaller scales, the increase in diversity with increasing fire frequency may simply be an artifact of plant size: very frequent fires select for small plants and more individuals are packed in a single plot (Oksanen 1996). Previous studies of fire and diversity have described similar patterns. In studies of Scottish heathlands, for example, Hobbs et al. (1984) found by comparing sites in the first season after burn, that sites that had experienced long intervals without fire had fewer species: the highest fire frequencies studied (6–15 years) produced the highest diversity. At larger spatial scales, the effect of decreased habitat heterogeneity with increasing fire frequency may swamp the effect of plant size. Collins

(1992) found a monotonic decline in grassland community heterogeneity with increasing fire frequency. Frequent burning might be expected to reduce habitat heterogeneity and therefore decrease community-wide species richness. Older vegetation, such as that at the low fire frequency sites before the 1989 burn, may have a more heterogeneous fuel load which can create patches of varying fire intensity during a burn. It is possible that such heterogeneity in fire intensity may cause specific responses in seed germination or recruitment among different fynbos species and lead to greater heterogeneity in post-fire vegetation. Bond and van Wilgen (1996) describe such possible mechanisms.

The fynbos shrublands of the Cape Province of South Africa have experienced periodic burning for at least 100 000 years, possibly since the early Pleistocene (Kruger 1979), and fire is currently used as a management tool to maintain biological diversity and watershed quality (Le Maitre 1987; Cowling & Gxaba 1990). Managers of fynbos have generally focused on preserving the prominent shrub species and have therefore considered fire intervals of about 15–25 years to be ideal (McLachlan & Moll 1976; van Wilgen 1982; Brown et al. 1991). Frequent burning of fynbos alters species composition by eliminating the large shrubs, mostly members of the Proteaceae, that do not have time to reach maturity between fires. Very long intervals between fires may likewise eliminate the largest shrubs because many of these proteoid species rely upon canopy-stored seed banks; the shrubs may senesce before fire allows their serotinous cones to open. The accumulation of dead biomass in old vegetation can also lead to more intense fires which may kill vegetation able to withstand less intense burns (Bond 1980; van Wilgen 1982). Although intermediate fire frequencies may preserve the large proteoid shrubs, this study found that such management will not necessarily preserve the largest number of species over a 0.1 hectare scale.

The deviation of the species-area curves from the expected semilog linear relationship in this study remains unexplained. Previous studies in fynbos have shown a linear relationship between species richness and log of sample area (Bond 1983; Richardson et al. 1989), and this semilog relationship has been reported from a variety of terrestrial plant communities (Shmida 1984; Miller & Wiegert 1989; Schafer 1990). When compared with the results of these previous studies, the species-area curves found in this study generally show lower species richness values at the 100 m² scale. Recent work in California using the same nested-

plot sample design indicates that post-fire chaparral, however, exhibits a similar deviation from the semilog relationship (Keeley, in press).

When data were plotted on a log-log scale, a significant linear relationship appeared (Figure 3). Although most plant diversity studies have shown linear species-area relationships on semi-log scales, Rosenzweig (1995) attributes this to problems of small sample size and suggests that the log-log linear relationship should be more common when sample sizes are sufficiently large. Rosenzweig (1995) notes that almost all animal species-area curves and plant species-area curves constructed from nested plots over very large areas approximate a straight line in log-log space. Although other studies in fynbos have used slightly different nested plot designs, it seems unlikely that differences in sampling procedure could account for the markedly steeper curves found in this study. A possible explanation for these unusually steep species area curves may be that the vegetation was younger than that sampled in previous fynbos studies; perhaps maturing fynbos masks the heterogeneity effects seen in younger communities.

The intermediate disturbance hypothesis does not seem to hold true at any spatial scale in this study. At the small scales, the effect of plant size likely affects species diversity: high fire frequencies lead to smaller plants and more individuals per site. At larger scales, the effects of heterogeneity in fuels and subsequent post-fire habitat heterogeneity may increase community-wide species diversity. The ability of vegetation to influence the nature of the disturbance itself may contribute to the failure of the intermediate disturbance hypothesis in fire-prone systems. This study suggests that patterns of diversity and disturbance in fire-prone shrublands might be very different from those that emerged in marine studies.

Acknowledgements

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