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What makes nutrient-poor mediterranean heathlands so rich in plant diversity?

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ABSTRACT

Mediterranean heathlands with extremely low soil-nutrient concentrations (the fynbos of South Africa and the kwongan of Australia) have plant species diversities several times greater than one would expect from their areas. A combination of three factors provides a sufficient explanation for these diversities: First, poor soils favour shrubs that are killed by fire and re-establish from seed ('seeders'). Otherwise, the frequent fires in most mediterranean heathlands favour shrubs that can re-sprout ('sprouters'). Second, the numeric dominance of seeders on poor soil lowers their extinction rates. Third, seeders have relatively short generation times and thus increased speciation rates. Elevated speciation rates coupled with depressed rates of extinction lead to enhanced diversities. We elucidate this scenario and discuss evidence that favours the first factor. The evidence comes from 23 previously unanalysed sample plots surveyed by R.H. Whittaker and from two supplemental data sets. In mature fynbos and kwongan, 90 and 93% respectively of the shrub cover belongs to shrubs that re-seed after fire. In maquis (Israel), chaparral (California) and matorral (Chile), the proportion is considerably smaller. Mature strandveld, a South African shrubland superficially like fynbos but with richer soil, has only 29% seeders, although it is physically adjacent to fynbos. We suggest that nutrient-poor soil may favour seeders because the extra investment in underground organs is not worth the cost: pulses of nutrients released by fire lie mostly on top of the soil, inaccessible to new growth sprouting from subterranean lignotubers or epicormic buds.

Keywords: biodiversity hot spot, fynbos, kwongan, seeder, speciation, sprouter.

INTRODUCTION

Two of the five regions of the world with mediterranean heathland vegetation, the fynbos of South Africa's Western Cape Province and the kwongan of Western Australia, abound with plant species. Each has 8000–8550 angiosperm species, with 68–75% of them being endemic (Cowling *et al.*, 1996). Based on their areas, they ought to have only about a third as many

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(Rosenzweig, 1995). Both of these heathlands figure prominently in the compendium of the world's most important areas of diversity, its 'silver-bullet' hot spots (Myers *et al.*, 2000).

Three other mediterranean heathlands have quite ordinary plant diversites (Cowling *et al.*, 1996). These are the maquis surrounding the Mediterranean Basin, the chaparral in California and Baja California, and the matorral in central Chile. What makes the fynbos and the kwongan so diverse compared with the other three heathlands?

Previous contributions have catalogued many similarities between the two floristic regions. But virtually all those who have investigated the matter have noted a single overriding similarity: both fynbos and kwongan occur on very old, weathered soils (Christensen, 1994). These soils have remarkably low inorganic nutrient concentrations (e.g. Lamont, 1992; Stock and Allsopp, 1992). In contrast, maquis, chaparral and matorral all grow on moderately fertile soils. It would appear that, somehow, the combination of a mediterranean climate (summers, dry and hot; winters, cool and wet) with very poor soil leads to the high diversities. But how?

In this paper, we advance the following explanation for the high diversity of fynbos and kwongan vegetation:

- Perennials in mediterranean heathlands may be distinguished as seeders or sprouters. Seeders are those species whose individuals (genets) usually (or always) die after a fire. Consequently, the species must re-establish itself from seeds. Sprouters, on the other hand, rarely die of fires, even severe ones. Instead, their genets burn back to ground level and then sprout up from epicormic buds or lignotubers.
- Where fire is a common disturbance, as it is in mediterranean heathlands, seeders have much shorter generation times than sprouters.
- Thus, where fire is a common disturbance, seeders tend to speciate faster and attain higher diversities than sprouters.
- Poor soil gives perennial seeders an ecological advantage over sprouters and annuals.
- Thus, the combination of fire and poor soil leads to landscapes covered with seeders. The numerical dominance of the seeders in these landscapes allows them to attain much higher steady-state diversities than those they achieve in other heathlands where rich soil keeps them scarce and magnifies their extinction rates.

Previous contributions have also noted the probable importance of high seeder speciation rates to the high diversities of the fynbos (Cowling and Holmes, 1992; Cowling *et al.*, 1994). However, as we shall see, seeders live in all mediterranean heathlands. If they have proliferated in one, why not in all? Our model answers this question by combining those high speciation rates with ecology.

Our model stems from a variety of experiences, information and inference. Here, we first sketch our model in some detail. This will lay out the logic. Then we examine three different empirical sources. None of these covers evolutionary time, so none allows for a test of comparative speciation or extinction rates. But, in these static pictures of heathlands, we found a number of the features that we built into our model.

Our first empirical source is one that we feel privileged to have had available. It is data from carefully designed vegetation surveys by the late Robert H. Whittaker. Whittaker collected these data in 20 × 50 m plots of mediterranean heathlands, but he did not survive to analyse the results. He surveyed South African fynbos, Israeli maquis, Californian chaparral and a heathy South African association called strandveld. (We will describe strandveld below. Whittaker's data from this association are illuminating.)

Whittaker counted both the number of individuals of each species and the percentage cover of each. In contrast, previous conclusions about the character of heathland vegetation depended on assessing the proportions of seeder and sprouter species. The extra information for percent individuals and percent-cover is novel and was crucial for our study. Whittaker did not survey in Chilean matorral or Australian kwongan. However, one of us (L.O.-W.) has collected transect data in kwongan, fynbos and maquis. We use these as our second source of data. To incorporate Chilean data into our study, we turned to a third source, data from matorral and chaparral collected by Parsons (1973).

We do not present these data as a test of our model. They cannot so serve, because, in part, they are its source. Moreover, because they are rather sparse, the view of heathlands that they suggest is merely qualitative and hypothetical. Their description of the comparative landscapes of heathlands will, no doubt, be refined and improved. But, based on them, on our own experiences, on our discussions with colleagues and on the similarity of some of their trends to those already well accepted by plant ecologists, we have confidence that they are not misleading us. We believe that the model they suggest is sufficiently worthy to deserve tests.

MEDITERRANEAN HEATHLANDS

Mediterranean heathlands are dominated by evergreen, sclerophyllous shrubs. They burn readily, as often as every 10 years in South Africa and Australia and, on average, as often as every 40 years in California (Cowling *et al.*, 1996). In some areas of the Mediterranean, grazing has replaced fire as the dominant disturbance, leaving an anthropogenically modified landscape (Zohary, 1962). In Chile, fires were probably infrequent historically, but are becoming more frequent through anthropogenic ignitions (Fuentes *et al.*, 1994).

After fires, the individuals (genets) of some heathland-shrub species re-sprout from subterranean lignotubers or epicormic buds, whereas the individuals of other heathland-shrub species die (Bond and Van Wilgen, 1996). These latter species must re-enter the community from the seed bank. We term the former species 'sprouters' and the latter 'seeders'. Sprouting shrubs are generally considered to be both dominant and numerically more common than seeders in maquis, chaparral, matorral and kwongan (Zohary, 1962; le Maitre and Midgley, 1992; Malanson and O'Leary, 1982; Fuentes *et al.*, 1994; Montenegro and Ginocchio, 1995). But they rarely dominate and are not always most common in fynbos (Kruger and Bigalke, 1984; le Maitre and Midgley, 1992). In part, this paper examines these common beliefs.

Much of the extraordinary diversity in fynbos and kwongan belongs to a few groups of closely related species, usually endemic to their heathland region. In fynbos, the Ericaceae (*Erica*), Proteaceae (*Leucadendron*), Rutaceae (*Agathosoma*) and Polygalaceae (*Muraltia*) have speciated exuberantly (Cowling and Holmes, 1992). In kwongan, the same is true of the Myrtaceae (*Melaleuca*, *Eucalyptus*), Proteaceae (*Grevillea*, *Hakea*), Leguminosae (*Acacia*), Epacridaceae (*Leucopogon*), Asteraceae and Stylidiaceae (Pate and Beard, 1984). Yet, closely related members of these same taxa occur in other, less diverse but heathy associations in Australia and South Africa. Hence, we do not believe that the unusual diversity of kwongan and fynbos can be attributed to the presence of unusual taxa. If the combination of frequent fire and poor soil of these systems evoked their high diversities, then these taxa did the job of diversifying merely because they were in the right place at the right time.

DETAILS OF THE MODEL

Where fire is a common disturbance, seeders have much shorter generation times than sprouters. Every fire hot enough to destroy a plant genet prematurely terminates its life. Because generation time, by any definition, is a positive function of lifespan, the generation time of seeders must be short wherever such fires are frequent. We present this rule as all-or-nothing – seeder or sprouter. Of course, fire sensitivity is a continuous variable among species, with more sensitive species having shorter generation times than less sensitive ones. But the rule also applies in the continuous case: more sensitive species should have shorter generation times than less sensitive ones. Clearly, this rule has nothing to do with annuals. Nor does it apply in landscapes where fire is so infrequent that plants generally die before exposure to one.

Seeders will see many more long-lasting barriers than sprouters and tend to speciate faster. Differences in generation time will be responsible for this tendency. Generation time plays a major role in determining a species' evolutionary response to a geographical barrier. For such a barrier to evoke a speciation event, it must last long enough for the species to respond genetically (Rosenzweig, 1975). How much is 'long enough' depends on the species, particularly on its generation time. Some barriers will last long enough for species that go through many generations per century, but not long enough for those that go through only one. Thus, in the presence of exactly the same set of geographical isolating barriers, species with short generation times will see more long-lasting barriers and produce more new species than species whose individuals live much longer lives (Fig. 1).

To illustrate the effect of generation time on species diversity, let us assume two equal-area independent regions, one with only seeders and the other with only sprouters. The one with seeders will have generation times perhaps one order of magnitude shorter than the one with sprouters. Let us further assume that, in other things, sprouters and seeders are fairly equivalent. In particular, let us assume that sprouters and seeders have about the same population sizes and geographical distributions and that therefore they share extinction probabilities. Then, the region with only seeders should attain higher steady-state diversities than the one with only sprouters (Fig. 2). However, all mediterranean heathland regions have mixtures of seeders and sprouters. Therefore, the model needs to consider how seeders and sprouters fare ecologically in each other's presence.

Let us first assume a single region that begins with equal proportions (50%) of seeder species and sprouter species. If seeders and sprouters enjoy equal ecological success, we will expect the average seeder to be about as abundant and widespread as the average sprouter (abundance is 'genets per unit area'). Under these circumstances, Fig. 2 again applies – seeder speciation rates outpace sprouter speciation rates. The proportion of seeding species will grow, but not to 100%. Assuming that the abundance and distribution of a seeder responds more to the diversity of other seeders than to sprouters, the growing diversity of seeders will make them scarcer and more narrowly distributed than sprouters. Eventually, this increased rarity and restricted distribution will cause seeder extinction rate to balance their higher speciation rate. At that point, the region will have many more species than it

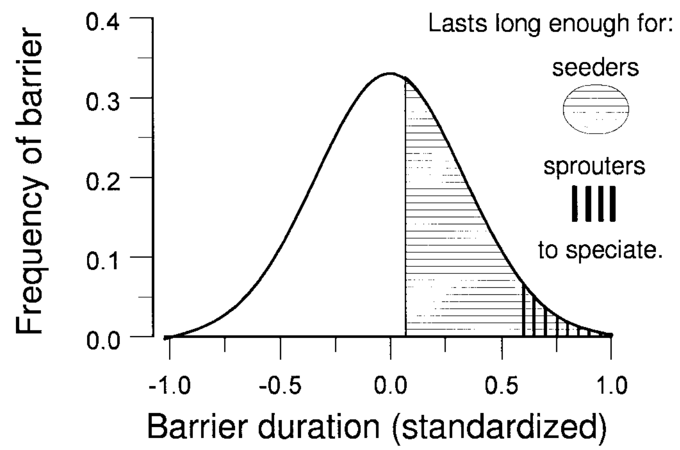

Fig. 1. Geographical barriers endure for a variety of times, modelled here as a normal distribution. Only some barriers endure enough generations for completion of speciation. Assume that the number of generations required for speciation does not depend on generation time. Then, species with shorter generation times will experience a greater fraction of barriers as long-lasting (i.e. leading to speciation). Where fires are frequent, seeders should have shorter generation times than sprouters and thus higher speciation rates. (*Note*: Thresholds in the graph are merely illustrative. We did not calculate the fraction of barriers that last long enough for either seeders or sprouters to speciate.)

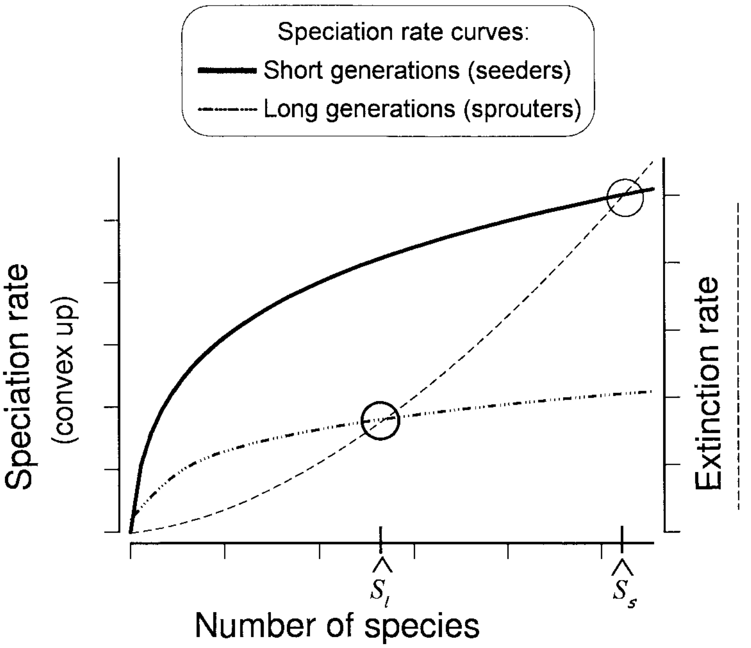

Fig. 2. Extinction and speciation rate curves for seeders and sprouters in a frequent-fire system. Fire reduces the generation time of seeders leading to a higher speciation-rate curve (——) and a higher steady-state diversity ($\hat{S}_s$). Based on provincial diversity theory (Rosenzweig, 1995).

would have had in the absence of the seeder strategy. Nevertheless, because neither has an ecological advantage, the sum of seeder species' abundances should be quite similar to the sum of sprouter species' abundances. Total coverages should also be similar.

Now let us consider a region in which seeders outperform sprouters ecologically. Here, the sum of seeder species' abundances (and their total coverage) will be more than the sum of sprouter species' abundances (and their total coverage). It will take more seeder species before their average abundance and range size is small enough to establish a steady state – that is, the diversity at which extinction matches speciation. At steady state, the region will have even more species than it would have in the previous region (where neither seeders nor sprouters had an advantage). Moreover, the relatively scarce, narrowly distributed seeder species will far outnumber sprouter species.

We do not claim that seeders must always outnumber sprouters. In a region where sprouters outperform seeders ecologically, the predicted proportion is not so clear. As seeder coverage declines from 50%, fewer and fewer seeder species will be needed to reduce average seeder abundance and range size to a steady state. The steady state will still have more species than it would have in the absence of the seeder strategy, but sprouter species may actually outnumber seeders. The point of ecological success at which the two types should maintain an equal diversity depends on many unknowns. Nevertheless, the point of ecological success that yields equal diversity should occur only in a region where sprouters have a decided ecological advantage.

In summary, total diversities should be correlated with the proportion of seeder species. It does not matter whether we measure that proportion as percent cover or percent species. With their higher speciation rates, seeders force regions to higher diversities than would otherwise occur. As ecological success shifts from sprouters to seeders, total steady-state diversity must also rise.

Note that another prediction has emerged from the model. If seeders speciate faster, then their ranges ought to get subdivided into finer bits and their geographical distributions ought to be more restricted than those of the sprouters with which they share a region. That should give seeders a higher average extinction rate than sprouters. As a result, at steady-state diversity, many seeders should be rather rare and narrowly distributed, regardless of total seeder diversity. These rare seeders will be the species contributing the high extinction rates that prevent diversity from growing further. Reseeders with large, widespread populations are, on the other hand, taxonomically unstable. They would have very low extinction rates and be targets of opportunity for rapid speciation. They should disintegrate into many species, each with restricted ranges. This last prediction does not depend on ecological success.

WHITTAKER'S DATA SET

Robert H. Whittaker and his associates surveyed 20 × 50 m plots from 1975 to 1979 in heathland vegetation in North America, Israel and South Africa. They sampled 50 such plots, but we used only the 23 identified in his site descriptions as either mature and relatively undisturbed or as disturbed. These included: eight plots in chaparral in the Santa Ynez and San Rafael Mountains, California and in Baja California, Mexico; five plots in maquis near Mt. Carmel, Mt. Meron and Haifa, Israel; five plots in fynbos near Ladismith, Humansdorp and Otterford in the Eastern Cape Province, South Africa; and four plots in fynbos in or near the Jonkershoek and Lebanon Forests in the Western Cape Province. The importance of being able to distinguish mature plots from those recently disturbed will become evident later.

We also include one plot of mature strandveld, or coastal heath vegetation, that Whittaker surveyed near Koeberg, South Africa. Strandveld grows on soil enriched by sea spray with nutrients. It thus occurs in a very narrow band (hundreds of metres wide) between the ocean and the fynbos. Fires sometimes stop at its edge, inhibited by higher humidities and the less dried out plants that live in its more moderate micro-environment. Otherwise, strandveld is a heathland superficially similar to fynbos.

Each Whittaker plot contained nested sub-plots 1 × 1 m, 1 × 5 m, 2 × 5 m, 2 × 10 m and 10 × 10 m in size (Shmida, 1984). Within each sub-plot, and within the 20 × 50 m plots, Whittaker identified and recorded all vascular plant species. Within each 20 × 50 m plot, he also estimated percent cover for each species. Sometimes he noted trace occurrences of a species. We assigned these the arbitrary abundance of 0.05%.

We assigned all plants to one of the following three groups: annual (including biennial), herbaceous perennial or woody perennial. We also sorted them according to their ability to survive fire. Annuals were considered seeders. Herbaceous perennials in chaparral and maquis were assumed to be sprouters following Keeley (1995) and Keeley and Swift (1995). Woody perennials that were identified in the literature as having the ability to survive fire were labelled ‘sprouters’, whereas those that are killed by fire and that re-enter the community from the seedbank were labelled ‘seeders’. Because the literature rarely differentiated further, our sprouter category included both obligate and facultative sprouters (*sensu* Naveh, 1975; Keeley, 1986). Facultative sprouters usually survive moderate fires, but not intense ones.

We obtained life-history information for chaparral species primarily from Jepson (1925), Van Rensselaer (1942), Sampson (1944), Wells (1962, 1972), Munz and Keck (1965), Munz (1968), Tratz and Vogl (1977), Wiggins (1980), Keeley (1981), Malanson and O’Leary (1982, 1985), Hickman (1993), Montenegro and Ginocchio (1995) and Zedler (1995, personal communication). We obtained similar information about maquis species primarily from Zohary (1962, 1966, 1972), Mouterde (1966), Naveh (1975), Feinbrun-Dothan (1978), Keeley (1995) and our own personal observations (L.O.-W. and A.S.). Our information on fynbos species came from Van der Merwe (1966), Kruger (1979), Bond and Goldblatt (1984), Frost (1984), Kruger and Bigalke (1984), Cowling (1992, personal communication), Van Wilgen and Forsyth (1992), Keeley (1995) and Schrire *et al.* (B. Schrire, T. Hoffman, A. Rebelo and F. Ojeda, personal communication).

Because disturbances affect species diversity (Grime, 1973, 1979; Grubb, 1977; Connell, 1978; Huston, 1979), we analysed mature and relatively undisturbed plots separately from recently burned or grazed plots. We used analyses of variance and *t*-tests (with Tukey’s, SNK and Bonferoni multiple comparisons procedures) to test for differences in the numbers of species and the proportions of different life-history types in plots from different mediterranean regions. Only a single strandveld plot was surveyed, so we did not include it in the multiple comparisons.

SUPPLEMENTARY DATA SETS

Transects were surveyed by one of us (L.O.-W.) in mature, relatively undisturbed kwongan, maquis and fynbos in 1983, 1981 and 1979 respectively. Each transect was a strip of 50 contiguous 1 × 1 m plots (50 m^2). Two such strips were positioned on Mount Leseur, Australia, Mount Meron, Israel and at Jakkalsrivier in the West Cape Province, South Africa. Within each 1 × 1 m plot, the presence or absence of all species was recorded. From this we calculated diversity by counting the numbers of species per 50 m^2. We also obtained a surrogate measure of percent cover by summing the number of occurrences of species of each life-history type. For example, 1108 occurrences of species of all types were recorded in one of the fynbos transects, and 173 of these were woody seeders (surrogate percent cover = 15.6%). Because the data set was smaller and fewer species were involved, we could identify species as seeders, facultative sprouters or sprouters. Seeders were defined as species that are killed by fire and that regenerate through germination. Facultative sprouters regenerate after fires both vegetatively and through germination, but may experience high mortality in intense fires. Obligate sprouters produce few if any seedlings and survive even quite intense fires.

Information on the life histories of kwongan species came from Marchant *et al.* (1987), Montenegro and Ginocchio (1995) and Enright *et al.* (N. Enright, T. Griffin, A. Hopkins and B. Lamont, personal communication). Additional information on the fire responses of maquis species came from Z. Naveh (personal communication) and for fynbos species from Adamson and Salter (1950) and R. Cowling and T. Rebelo (personal communication). Statistical analyses were not performed on these data because, on Mount Leseur and Mount Meron, the transects were bisected strips 100 m long, whereas, at Jakkalsrivier, the two 1 × 50 m strips were not adjacent.

To include the matorral, we turned to Parsons (1973). He compared 100 m^2 plots of mature, relatively undisturbed heathland in Echo Valley, California ($n = 364$) and in Fundo Santa Laura, Chile ($n = 206$). In each plot, he listed all woody species that were present. For true shrubs (excluding woody vines and suffrutescent semi-shrubs), he also recorded a numeric cover degree-abundance value. By totalling these for all species of one life-history type from all plots, we obtained a surrogate measure of percent cover. Because of the data set's small size, we were again able to identify the species as seeders, facultative sprouters or obligate sprouters. Additional information on the life histories of chaparral shrubs came from Parsons (1973), Keeley (1977, 1986), Sauer (1977), Tratz and Vogl (1977), Zedler (1977, personal communication), Keeley and Keeley (1981) and Keeley and Zedler (1978), and for matorral shrubs from Parsons (1973), Keeley and Johnson (1977), Keeley (1986) and G. Montenegro (personal communication).

CHARACTERISTICS OF THE DATA

Species diversity

The literature states that fynbos and kwongan each have more species than chaparral, matorral or maquis. The mature vegetation we examined did not challenge this. Within the 1000 m^2 Whittaker plots of mature vegetation, fynbos was more diverse than chaparral and maquis, with no significant difference in diversity between the latter two ($P = 0.0001$, Table 1). In 50 m^2 areas of mature vegetation (Table 2), fynbos and kwongan had similar diversity, but was more diverse than maquis. Parsons' chaparral and matorral data from 100 m^2 plots (Table 3) reveal their similar diversity. (Note that because the three tables come from three different sample methods, we cannot compare the numbers of one to another.)

Significant differences between heathland regions did not emerge in the plots with

Table 1. Numbers and abundances of vascular plant species in mature chaparral (California), maquis (Israel), fynbos (South Africa) and strandveld (South Africa) vegetation[a]

	Number (%)				Cover (%)			
	Chaparral (14.0)	Maquis (31.5)	Fynbos (62.4)	Strandveld (33.0)	Chaparral	Maquis	Fynbos	Strandveld
Annuals	22.1	2.7	2.8	3.0	7.0	0.1	0.3	0.1
Herbaceous perennials								
seeders	0.0	0.0	1.9	0.0	0.0	0.0	0.6	0.0
sprouters	12.2	42.8	32.8	6.1	1.4	1.2	29.9	9.5
unknown	0.0	0.0	15.3	6.1	0.0	0.0	7.3	0.3
Woody perennials								
seeders	11.4	1.4	15.8	21.2	7.3	tr	52.6	20.7
sprouters	33.9	46.6	11.1	21.2	81.8	98.4	6.5	51.8
unknown	18.9	6.6	20.1	42.4	2.0	0.2	2.8	17.6
Unknown	1.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0

[a] The vegetation was surveyed using Whittaker plots (20 × 50 m). We used five pseudo-replicates of chaparral and fynbos, two of maquis. Only one of strandveld was available. The average number of species per plot is given in parentheses. Percent cover is a summation of the estimates for all species within the life-history type. Amounts less than 0.1% are indicated by ‘tr’ (trace).

Table 2. Numbers and abundances of vascular plant species in mature maquis (Israel), fynbos (South Africa) and kwongan (Australia)[a]

	Number (%)			Cover (%)		
	Maquis (26.5)	Fynbos (74.0)	Kwongan (73.0)	Maquis	Fynbos	Kwongan
Annuals	0.0	0.6	1.4	0.0	tr	0.2
Herbaceous perennials						
seeders	0.0	1.4	8.2	0.0	0.1	14.0
sprouters	22.0	41.2	15.8	13.0	45.0	21.4
unknown	0.0	10.4	8.9	0.0	13.4	4.7
Woody perennials						
obligate sprouters	29.5	2.1	2.7	31.8	3.2	3.6
facultative sprouters	30.4	4.0	28.8	41.2	2.2	36.3
seeders	1.6	16.9	12.3	1.4	17.8	11.8
seeders or facultative	0.0	7.9	0.0	0.0	11.8	0.0
unknown	5.4	8.8	21.2	4.5	2.8	7.6
Unknown	11.0	6.7	0.7	8.3	3.6	0.2

[a] The vegetation was surveyed using 1 × 50 m line transects with two pseudo-replicates per location. The average number of species per transect is given in parentheses. Percent cover is the accumulated total of all the occurrences of each species within a life-history type. Amounts less than 0.1% are indicated by 'tr' (trace). Because little is known about some fynbos species, we added an extra category for those species that are either seeders or facultative sprouters.

Table 3. Numbers and abundances of woody perennials in mature chaparral (California) and matorral (Chile)[a]

	Number (%)		Cover (%)	
	Chaparral (5.9)	Matorral (7.4)	Chaparral	Matorral
Seeders	13.0	5.8	17.8	1.5
Facultative sprouters	17.4	1.9	33.5	5.8
Obligate sprouters	28.3	73.1	38.0	82.1
Unknown	41.3	19.2	10.8	10.6

[a] Plot size: 10 × 10 m. The average number of shrub species per plot is given in parentheses. Data from Parsons (1973). Percent cover is the summation of the numeric cover degree-abundance values for all species within a life-history type.

disturbed vegetation (Table 4) ($P = 0.2979$ for these 1000 m^2 plots). Disturbed sites had recently been burned, grazed or both.

We had not anticipated the similarity of disturbed heathlands. At first, we analysed the data without separating the mature plots from the disturbed ones. In that mixed state, the data seemed to deny any significant difference between the regions' diversities. Thus, the data suggest that the difference between heathlands is a difference in mature diversities only – that is, diversities that develop as a place recuperates from a disturbance.

Table 4. Numbers and abundances of vascular plant species in disturbed chaparral (California), maquis (Israel) and fynbos (South Africa)[a]

	Number (%)			Cover (%)		
	Chaparral (56.0)	Maquis (93.0)	Fynbos (80.8)	Chaparral	Maquis	Fynbos
Annuals	51.9	55.4	1.6	40.7	21.5	0.1
Herbaceous perennials						
seeders	0.0	0.0	3.7	0.0	0.0	5.6
sprouters	17.3	24.7	32.0	10.9	8.2	35.5
unknown	0.0	0.0	15.2	0.0	0.0	6.4
Woody perennials						
seeders	1.3	4.1	14.6	0.1	5.8	19.0
sprouters	15.7	7.4	14.6	44.7	63.7	30.6
unknown	8.4	2.4	18.2	3.3	0.3	2.7
Unknown	5.4	6.0	0.0	0.3	0.6	0.0

[a] The vegetation was surveyed using Whittaker plots (20 × 50 m) with three pseudo-replicates of chaparral and maquis, four of fynbos. The average number of species per plot is given in parentheses. Percent cover is a summation of the estimates for all species within the life-history type.

Figure 3 shows Whittaker's chaparral plots. As they mature after fire, they lose 75% of their diversity. Maquis plots seem to lose almost as much diversity (about two-thirds). Grazed chaparral plots also have more species than mature ones, about as many as half-recovered post-fire plots (Fig. 3). In contrast, the diversity of a fynbos plot does not appear to decline very much as it recuperates from fire (about 23%; compare Tables 1 and 4).

Disturbed sites were more variable than mature sites. We attribute their higher variability to the different kinds and intensities of disturbances that had affected the sites, although that is merely a conjecture.

Vegetation composition

Do the data shown in Tables 1–3 suggest any similarities in the mature landscapes of the diverse heathlands that differentiate them from their less diverse analogues? They do. The richer regions have more herbaceous perennials and a lower proportion of woody obligate sprouters. In contrast, mature sites in all regions seem to have few annuals.

Straightforward examination of Tables 1 and 2 reveals that large numbers of herbaceous perennials persist in the mature vegetation of fynbos and kwongan. They covered 37.8% of the Whittaker plots in the fynbos, 58.5% of the area of the fynbos transects and 41% of the area of the kwongan transects. Maquis and chaparral never had more than 13% cover by herbaceous perennials and, in the Whittaker plots, barely scored over 1%. In addition, both fynbos and kwongan have obligately seeding herbaceous perennials. Although not a large element of the vegetation, they are entirely absent from the other three mediterranean heathlands.

The pattern in woody plants is not so transparent for two reasons. First, it comes from all three tables. Second, it involves an additional complication – the difference between obligate

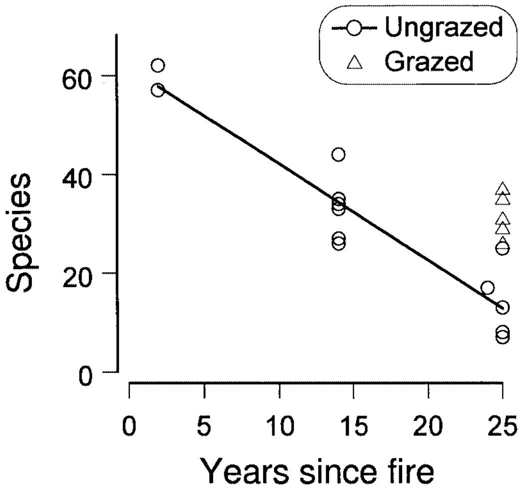

Fig. 3. Disturbance (grazing or recent fire) increases diversity. Chaparral vegetation declines as a plot recovers from fire ($R^2 = 0.88$; $P = 0.000001$). Grazed plots have more species than mature, undisturbed plots ($F = 26.2$; d.f. = 9; $P = 0.00063$). We position grazed and mature plot diversities above the 25-year mark arbitrarily; we do not know the actual time since they last burned.

and facultative woody sprouters. Recall that facultative sprouters usually survive moderate fires, but not intense ones. Therefore, a facultative sprouter should have a generation time shorter than that of an obligate one, but not as short as that of a seeder. We might suspect interesting differences between regions based on this distinction; however, we were unable to distinguish obligate from facultative in Table 1 and could not always do so for Tables 2 and 3. In many cases, we did not even know whether a plant was a seeder or a sprouter.

To aid our analysis, we compiled Table 5. We restricted it to plants that we could specify as seeder or sprouter (from Table 1), or seeder, facultative sprouter or obligate sprouter in the other tables. We used the woody cover values for two reasons. First, they had very small percent-unknowns. In addition, the discrepancies in percent cover between Whittaker's data and the supplementary data could result from the different measures of cover used in the three sample sets. A woody shrub is usually larger than an herbaceous perennial. Mere 'presence' will fail to account for this size difference and lead to an underestimation of the true percent cover of woody plants in the supplementary data sets. This problem, however, does not influence relative values of the different life-history types within total shrub cover. Thus, in Table 5, we ranked the percentages of woody plant cover known to have one or another method of regeneration after fire.

Seeders and facultative sprouters, when considered together, dominated both fynbos and kwongan (90.1 and 93% respectively), but were less prominent in maquis (57.3% in the same data set). Seeders and facultative sprouters also covered much less ground in chaparral and, in particular, matorral. Although the latter two percentages come from a different source, note the similar values of chaparral in Tables 1 and 3 with respect to percent-seeder coverage. This similarity suggests that adjustments for source differences would not affect the rankings.

Table 5. Woody plants whose method of regeneration after fire is known: plot types ranked according to percentage cover[a]

Seeders (%)	Source	Seeders and facultative sprouters (%)	Source
89.0	Fy1	93.0	Kw2
67.8	Fy2	90.9	Fy2
28.6	St1	58.4	Ch3
22.8	Kw2	57.3	Mq2
19.9	Ch3	8.2	Mt3
8.2	Ch1		
1.9	Mq2		
1.7	Mt3		
0.0	Mq1		

[a] Source number refers to the previous table number. Fynbos and kwongan show consistently high percentages of seeders or facultative sprouters, regardless of the data source. *Note*: fynbos2 percent seeders comes from adding half the 33.7% of woody cover known to be either facultative sprouter or seeder to the 50.9% known to be seeders.

By themselves, woody seeders contributed more to cover than sprouters only in the fynbos (89% in Table 1, 67.8% in Table 2). The kwongan's percent seeders was much less (22.8%), not so very different from those of strandvelt or chaparral. Therefore, although the very high seeder percentage by itself characterizes the fynbos, apparently it is the combination of seeders and facultative sprouters that set the two diverse heathlands apart from their analogues.

The disturbed vegetation of the Whittaker plots yielded quite a different set of results. In all mature sites except one (fynbos in Jakkelsrivier), woody species accounted for most cover. But the data from disturbed chaparral, maquis and fynbos all showed declines in that percentage: in chaparral from 91.1 to 48.1%; in maquis from 98.6 to 69.8%; and in fynbos from 61.9 to 52.3%. This left the fynbos' shrub cover looking much like the chaparral or maquis, except that many more of the fynbos shrubs were seeders.

Of course, annuals and herbaceous perennials accounted for the difference between mature and disturbed woody percentages. However, in maquis and chaparral, it was the annuals that expanded and by quite a bit. In fynbos, it was perennial herbs, although only very slightly so. Even in the face of a disturbance, the fynbos does not appear to support much annual plant cover or diversity. We suspect the same may be true of kwongan, although none of our data sets bear on this issue. Mature kwongan certainly has a low percentage cover of annuals, although so does mature maquis.

Although Table 4 cannot tell us whether any features of disturbed vegetation are shared between fynbos and kwongan, it does point to fascinating ecological dynamics when coupled with Table 1. As the result of a fire, woody vegetation retreats and woody seeders, in particular, are hard hit. Since, by definition, the fire kills all woody seeders, one ought to expect that retreat. Note, however, that the results show the differences in fynbos to be due largely to loss of size – the percentage of individual woody seeders in a fynbos plot is about the same before and after a fire. In fact, with respect to their percentages of individuals, fynbos plots hardly change after fire! Despite the destruction of most of their genets, they are paragons of stability. The small individuals present after a fire merely grow to adult size to bring about their changes to percent cover.

Compare this fynbos stability with the substantial physiognomic changes that occur in maquis or chaparral. Although many of their individuals are sprouters, a fire brings massive changes in the proportional make-up of their vegetation. This, as we have seen, derives largely from their prodigious increase in annuals.

From Tables 1 and 4, we can see a developmental trajectory common to maquis and chaparral and well known in plant succession. Early stages are replete with annuals. As perennials grow, the annuals diminish considerably. Seeders, although not truly rare in chaparral, never succeed there, unlike sprouters.

In contrast, there appears to be little succession in fynbos. Sprouters do not use their head start to dominate seeders. Annuals are never numerous. Herbaceous perennials, whether sprouters or seeders, and woody perennials, whether sprouters or seeders, maintain about the same relative numbers as a plot matures.

DISCUSSION

The data sets provide a picture of mediterranean heathlands somewhat different from what we had expected. Although fynbos and kwongan have more species than chaparral, matorral or maquis, the difference is concentrated. Woody vegetation and seeder herbacious perennials are the vegetation types that show it. The number of woody species in fynbos significantly exceeded that in chaparral or maquis ($P = 0.0002$), but the fynbos had numbers of woody shrubs similar to those in kwongan. Meanwhile, fynbos and kwongan annuals are much less diverse than their counterparts in other heathlands.

Not only is the difference concentrated in a few life forms, it is also concentrated in time. Recently disturbed patches of heathland have much the same diversities regardless of the continent on which they grow. As they recuperate, those from fynbos lose few of their species, whereas those from maquis or chaparral decline significantly. Specht (1981) reported a similar large decrease in the diversity of an Australian shrubland in South Australia (well east of the kwongan). After fire, plots (of unspecified size) declined from 38 to 11 species in 50 years.

Whittaker's sample plots demonstrate the importance of knowing the disturbance histories of communities that are to be compared. For example, chaparral is reported in the literature as supporting 31 ± 10 species in 1000 m^2 (see review in Cowling *et al.*, 1996), a value very close to the mean of Whittaker's values of 56 ± 7 and 14 ± 11 species for disturbed and mature chaparral respectively, but different from either of them. Likewise, the reported value for maquis of 70 ± 54 species in 1000 m^2 (Cowling *et al.*, 1996) agrees with the mean of Whittaker's values of 93 ± 28 and 32 ± 6 species for disturbed and mature maquis. There is less of a problem with the diversities of fynbos plots because these do not change much while plots recuperate after fire. Whittaker's values of 81 ± 45 and 62 ± 21 species in disturbed and mature fynbos, respectively, agree with the literature's value of 70 ± 21 species in 1000 m^2 (Cowling *et al.*, 1996).

The data we looked at support the connection between diversity and soil nutrient concentrations. Of course, they must with respect to continental differences, but they also do so within South Africa itself, as the strandveld plot shows.

The strandveld of South Africa is a narrow strip of heath growing along the coast. Although its soil is fully as old and leached as that of the fynbos abutting it, it has ordinary plant diversity. Richard Cowling (personal communication) let us in on that secret and why it is so important. And we see it exemplified in the single Whittaker plot we had available. Despite its plants coming from the same genera and families as those of the fynbos, it was only about half as diverse, similar in fact to maquis. What does this have to do with soil nutrients? Recall that sea spray enriches the soil in which strandveld grows. This may not be the only difference – strandveld also does not burn as often or as intensely as fynbos. However, it does suggest that the nutrient–fire connection to high plant diversity is probably correct.

Vegetational differences between strandveld and fynbos also parallel the differences one sees between rich and ordinary heathlands. Strandveld and fynbos share similar numbers of woody species and similar numbers of individual seeder and sprouter shrubs. However, unlike fynbos, strandveld is dominated by its sprouting shrubs. Seeders made up only 28.6% of its known woody cover compared with the 89% of fynbos (Table 5). Although physically adjacent to fynbos and with species in common, strandveld's dominant growth form resembles that of maquis or chaparral rather than fynbos.

Whittaker's data (from three of the five mediterranean heathlands) exemplified the increased importance of reseeding in the fynbos. Seeder shrubs occur in mature fynbos, maquis and chaparral, but only in the fynbos do they contribute more to cover than sprouters. Likewise, only in the fynbos are seeders more numerous than sprouters. The literature usually agrees, albeit by counting taxa (e.g. Zohary, 1962; Malanson and O'Leary, 1982; Kruger and Bigalke, 1984; le Maitre and Midgley, 1992; but see Keeley, 1986).

From the supplementary data (Table 2), we see that the kwongan also has seeding shrubs, but they are not as common as sprouters or as numerous. Nevertheless, in the kwongan, facultative sprouters outnumber and outcover obligate sprouters by a ratio of about 10 : 1 (Table 3; see also Pate and Beard, 1984; le Maitre and Midgley, 1992). In contrast, facultative sprouters and obligate sprouters are about of equal importance in both chaparral and maquis. In matorral, obligate sprouters outcover facultative sprouters by 14 : 1 and outnumber them by almost 40 : 1, quite the reverse of the kwongan situation.

Specht (1981) reported that Australian shrublands outside the kwongan also show a dominance of resprouting. Sprouter percentages of total biomass in eight heaths ranged from 54.2 to 93.4% (and the lowest two of the eight percentages are likely to be underestimates because of their high percent unknowns). In another study at a smaller geographical scale in Victoria, eight plots of heath returned similar, but slightly higher values (about 64–98%) of sprouter biomass (Specht, 1981). As in the case of strandveld versus fynbos, these heaths consist of plants closely related to their cousins in the highly diverse heaths of the kwongan.

Since facultative sprouters are often killed by fire and reproduce from seed, they also may have short generation times. Thus, it does not matter whether a species *can* resprout but whether it *does* resprout. Usually, if it does not, then it is functionally a seeder. It will have nearly as short a generation time and nearly as fast a speciation rate as if it could not resprout at all. Thus, because shrubs in Australia re-establish 'rarely, strictly by resprouts' (Keeley, 1995), the shrubs of both fynbos and kwongan are functionally similar after all.

Herbaceous perennials provide more insight into the importance of the seeder life history for fynbos and kwongan heathlands. Both have obligately seeding herbaceous perennials (Kruger, 1977; A. Hopkins, personal communication; see Tables 1, 2 and 4). This life-history type is entirely absent (or unknown) in chaparral, matorral and maquis (e.g. Naveh, 1975; Keeley, 1986), as well as in strandveld. Therefore, independent of taxon, herbaceous heathland seeders occur only in the two infertile, species-rich heathlands of Australia and South Africa.

The evidence from the strandveld and the five mediterranean heathlands leads to the hypothesis that resprouting after a fire works better than reseeding on fertile soils, but that the reverse is true on infertile soils. Why should seeders have an ecological advantage where soil has only the tiniest of nutrient concentrations? Cowling and Holmes (1992) suggest that reseeding may be of no inherent advantage, but may be common because the taxonomic lineages that contain reseeding species also possess other traits that promote speciation, for example microsymbiont-mediated nutrient uptake, serotinous cones and seed dispersal by ants (Lamont *et al.*, 1991; Cowling *et al.*, 1994; McDonald *et al.*, 1995). However, that view leaves us with a mystery.

As we have seen, seeders are not limited to fynbos and kwongan, but also occur in heathlands of ordinary diversity. For example, Wells (1969) noted the substantial diversity of seeders in chaparral. If reseeding confers no special advantage, but is merely associated with rapid speciation, why have not the other heathlands developed high diversities similar to those of fynbos and kwongan? This question seems especially embarrassing for the strandveld, which, after all, starts out with the same lineages as the fynbos, but fails to achieve fynbos diversities. If we were its mother, should we be mortified at its wasting of the family genes? Or, had we better excuse it as having made the most of a different environment? Moreover, our data show a characteristic that mere diversities of seeders cannot explain.

The ratio of percent cover to percent individuals is an index of the relative size of genets. Although the supplementary data contain only surrogates for percent cover, Whittaker did measure it. Thus, we could calculate the relative size indices of Tables 1 and 4. In recently disturbed plots, sprouters have the higher indices, showing that they do get a head start (Table 6). They maintain that advantage in chaparral and maquis. Mature strandveld has ratios like chaparral and maquis. But a seeder individual in a mature fynbos plot is much larger than a sprouter. Starting, in recently disturbed plots, at little more than half the size of a sprouter, it grows to cover almost six times as much area as a sprouter in a mature fynbos plot. To us, that appears to be a signal that seeding is advantageous where the soil is quite poor, but sprouting wins where soil is rich.

We propose that, in the very infertile soils of the fynbos, resprouting after a fire costs more than it is worth. Fires release some nutrients but also cause others to run-off, be eroded or be volatilized (Van Wyk *et al.*, 1992). In addition, the nutrients that are released after a fire will be very shallow, perhaps too shallow to be accessible to new growth sprouting from subterranean lignotubers or epicormic buds, but available more readily to seedlings (Naveh, 1994). Resprouters may therefore have difficulty finding the nutrients needed to replace the tissue they have lost to the fire. Finally, the cost of maintaining the surviving root mass in the absence of leaves may be high, especially as sprouting shrubs have root-to-shoot ratios higher than seeders (Dodd *et al.*, 1984; Moreno and Oechel, 1994; Canadell and Zedler, 1995).

Annuals, too, tell a story that fits with our view of the way nutrient deficiencies alter the composition of the fynbos. In recently disturbed chaparral and maquis, diversity is high because a large number of annuals appear and cover a substantial proportion of the ground (Table 4; see also Naveh and Whittaker, 1979). Annuals flourish in the increased light levels of the defoliated canopy and from the increase in nutrients that follow fire. Yet, almost no

Table 6. Relative size indices of woody plant genets in different heathlands from Whittaker's plots[a]

	Fynbos	Maquis	Chaparral	Strandveld
Recently disturbed				
Seeders	1.30	1.41	0.08	—
Sprouters	2.10	8.61	2.85	—
Mature				
Seeders	3.33	0.04	0.64	0.98
Sprouters	0.59	2.11	2.41	2.44

[a] The relative size index is the ratio of percent cover to percent individuals.

annuals grow in recently disturbed fynbos, with its similar increased light levels and similar high diversity (see also Cowling, 1983). Instead, one finds herbaceous perennials, many of which persist as the fynbos matures (Table 1).

We attribute the virtual absence of annuals to the infertile soils of the fynbos. Probably, their nutrient resources are too low for annuals to complete their life cycles and set seed in one growing season (Harper, 1977; Keeley, 1986; le Maitre and Midgley, 1992). In the virtual absence of annuals and with reduced competition from sprouting shrubs, herbaceous perennials and the seedlings of seeding shrubs can flourish.

Cowling *et al.* (1992) and McDonald *et al.* (1995) identify the typical endemic fynbos species as a non-sprouting dwarf or low shrub with a persistent seed bank and ant-dispersed seeds. Reseeding shrubs typically have large, ant-dispersed seeds rather than wind- or vertebrate-dispersed seeds (Keeley, 1981; Cowling *et al.*, 1992). As a consequence, they re-invade fire-scarred areas very slowly. For example, ants disperse one fynbos species, on average, only 2.5 m per generation (Slingsby and Bond, 1984). For such plants, widespread fires can be geographical isolating barriers. More traditional sorts of geological discontinuities will be optional for speciation and may come only as infrequent events.

This leads to a recapitulation of our scenario for high plant diversities in nutrient-poor, fire-prone mediterranean heathlands. The poor soils lead to the dominance of actual or functional seeders – shrubs and perennial herbs. Fires curtail their generation times, allowing large fires to act as long-lasting isolating barriers. They increase in diversity until becoming rare enough and local enough to have the high extinction rates that will counterbalance their high speciation rates. Seeders on rich soils have high speciation rates too, but they are so dominated ecologically by sprouters that they suffer high extinction rates and equilibrate at much lower diversities.

In 1977, Whittaker concluded that the study of species diversity would not reveal 'unifying principles and quantifiable relationships that could apply to all groups'. He thus turned away from his search for global generalizations and towards the investigation of local patterns of richness that are 'subject . . . to observation and evolutionary interpretation' (Whittaker, 1977; Westman and Peet, 1985). Here, by following his very own recipe, we see that he may have been too pessimistic. Mature mediterranean heathlands with very low soil fertility appear to have high plant species diversity as a consequence of elevated rates of speciation. Thus, they exemplify the general principle that we will discover the reasons for large-scale diversity differences by studying relative rates of speciation and extinction. That implies the value of another generalization: speciation and extinction rates combine to produce steady states that actually do govern diversity at a regional or bioprovincial scale.

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