

# Forecasting rain for groundnut farmers— How good is good enough?

Sulochana Gadgil<sup>\*</sup>,<sup>†</sup>, P. R. Sheshagiri Rao<sup>\*</sup>, N. V. Joshi<sup>\*</sup>, S. Sridhar<sup>†</sup>

<sup>\*</sup>Centre for Ecological Sciences, <sup>†</sup>Centre for Atmospheric Sciences, Indian Institute of Science, Bangalore 560 012, India

We illustrate how climatological information about adverse weather events and meteorological forecasts (when available) can be used to decide between alternative strategies so as to maximize the long-term average returns for rainfed groundnut in semi-arid parts of Karnataka. We show that until the skill of the forecast, i.e. probability of an adverse event occurring when it is forecast, is above a certain threshold, the forecast has no impact on the optimum strategy. This threshold is determined by the loss in yield due to the adverse weather event and the cost of the mitigatory measures. For the specific case of groundnut, it is found that while for combating some pests/diseases, climatological information is adequate, for others a forecast of sufficient skill would have a significant impact on the productivity.

THAT the agricultural productivity in our country is intimately linked to the vagaries of the monsoon has been known for centuries. In fact, the Indian economy has been said to be a gamble on the monsoon. The most important climatic element for agriculture in the tropics is the rainfall. The agricultural productivity depends on the total quantum of rainfall received in a year/season as well as its distribution within the year. The regions most susceptible to inter-year and intra-year variability are the semi-arid and arid regions. Management practices which take into account the rainfall variability over the region of interest are likely to generate a substantial increase in the sustained productivity<sup>1</sup>. In addition, if it becomes possible to forecast critical events (such as dry or wet spells) and take timely preventive measures, we expect a further increase in yields.

From the century-long meteorological data set available with the India Meteorological Department, the climatological information regarding the probabilities of occurrence of the important features of the rainfall profile (e.g. wet or dry spells) can be derived. Also, with the rapid development of general circulation models over the last two decades, it will soon be possible to generate reasonable forecasts over the medium range (3–10 days) for meteorological subdivisions of India. Establishment of the National Centre for Medium-Range Weather Forecasting at New Delhi has given major thrust to generating such forecasts using the country's

first supercomputer. At this stage it is important to consider how the climatological information/meteorological forecasts can be used for developing optimum cropping and management strategies. It is also necessary to spell out how good a forecast should be for it to be useful in a particular context. We address these questions in this paper.

To illustrate how climatological information and meteorological forecasts can be used to decide between alternative strategies, we consider the example of the productivity of groundnut in the red sandy soil of Karnataka and in the adjoining regions of Andhra Pradesh. Agroclimatology of groundnut, an important crop of the semi-arid tropics and a major source of edible oil, has been extensively studied<sup>2</sup>. The adverse weather events which can lead to a substantial loss in the productivity of rainfed groundnut are the dry and wet spells. The impact of prolonged dry spells on the yields in rainfed farming is well known. However, the impact of prolonged wet spells on the pests and diseases and on the productivity of the crops has received less attention. In fact, remedial measures to combat pests and diseases are more readily available to the farmer than those required to overcome the adverse effects of prolonged dry spells. Virmani<sup>2</sup> has suggested that effective use of weather and climatological information could be of great benefit to the groundnut farmers.

The adverse weather events promoting some of the major pests and diseases, leading to loss of productivity in groundnut, the typical losses incurred, as well as costs of possible mitigatory measures are discussed in the next section. Next we consider how climatological information about the adverse weather events, such as wet spells, can be used in deciding between alternative strategies, and discuss whether better results could be obtained with the use of forecasts for the specific season. We show that until the skill of forecasting such an event, i.e. the probability of correctly forecasting the event, is above a certain threshold (which is determined by the loss incurred due to the event and costs of mitigatory measures), the optimum strategy is the same as the one derived from climatological information alone. The agricultural situation thus places limits on the minimum skill of forecasts. It is shown that for groundnuts, the values of the cost-loss ratio involved

in measures against different diseases imply different strategies of management. A summary of the results and the general implications of the analysis are presented in the final section.

### Impact of adverse weather events on the productivity of rainfed groundnut

We consider here the Chitradurga District of the Karnataka State, which is located in the heart of the rainfed groundnut region. This region is characterized by regular monocropping of groundnut in vast areas with often the same variety, viz. TMV-2 (ref. 3). The crop is generally sown in July and harvested towards the end of about 120 days. This synchronized sowing leads to uniform crop growth stages over large areas and promotes the growth of certain epidemic pests and diseases. This problem is further accentuated by cultivation of groundnut in irrigated lands during summer, which implies the presence of host plants throughout the year<sup>4</sup>. Not surprisingly, the productivity of the rainfed groundnut in this region is critically dependent on the incidence of pests and diseases<sup>5</sup>.

As with other epidemic pests and diseases, the organisms are always present at a low level of intensity and can multiply rapidly when the weather conditions are favourable and the plant susceptible to attack. The dry spells promote the incidence of leafminer attacks and wet spells that of crown rot, late Tikka disease and collar rot. Losses in yields of pods and straw of groundnut by pests and diseases are variable, depending on the intensity of the attack and the crop growth stage during such an attack. Estimates of typical losses in yields with incidence of the different pests/diseases discussed here and the costs of plant protection measures are given in Table 1.

The main features of the rainfall profile at Chitradurga were derived from the daily rainfall data for 1901–90 supplied by the India Meteorological Department. The average rainfall pattern at Chitradurga on the weekly scale during April–December is depicted in Figure 1. Note the two clear peaks of the weekly rainfall in the pre-monsoon season in May and near the end of summer monsoon from mid-September to mid-October. The normal range of variation of rainfall in any week is also indicated in Figure 1 by solid bars, which extend from the minimum assured rainfall (at 75% probability) to the upper limit of rainfall (again for 75% of the years). Note that this range of variation extends all the way from zero rainfall to about 2–3 cm in May–June and again from mid-October to mid-November. The range is smaller during July–mid-September but is maximum from mid-September to mid-October. The cropping pattern for the region should be tailored for this rainfall profile and its variability.

Given the low average rainfall and high variability over this region, a week with 1 or 2 cm of rainfall can be considered to be a wet week. The probabilities of a wet week with rainfall greater than 1 cm or 2 cm are depicted in Figure 2a. The probabilities of no rain at all (0 cm) and of rainfall less than 0.25 cm in a week are shown in Figure 2b. We find that the probability of wet spells is highest for mid-September to mid-October, but since the variability is very large in October, the probability of dry spells is also not small.

For defining precisely, in terms of rainfall, what constitutes a wet spell that can promote the incidence of a specific pest/disease like late Tikka disease or crown rot, a detailed knowledge of the relationship of the intensity of the attack to the rainfall profile is required. In the absence of detailed quantitative information we base our definition of a wet spell and dry spell on the experience of one of the co-authors (PRS), who is also a farmer from this region. We take an intense wet spell to be one in which there is 2 cm or more of rainfall in two successive weeks. We take a dry spell as one in which there are two successive weeks with less than 0.25 cm of rainfall. The probabilities of successive weeks with wet/dry spells during the growing season July–December are given in Table 2. Groundnut is usually sown in July after the occurrence of sowing rains, i.e. about 1 cm per week. The probability of receiving such rains exceeds 50% in the second week of July (Figure 2) and remains high for the rest of the month. Generally, sowing is done in the second week of July. In Table 2 the different stages of the growth of groundnut are depicted assuming this period for sowing.

If a wet spell occurs at the seedling stage, namely 2–3 weeks after sowing (probability 0.13–0.16 from Table 2), waterlogging of the soil can lead to a high incidence of crown rot, causing rotting of young seedlings<sup>6</sup>. Crown rot in groundnut is caused by *Aspergillus niger*, which is a soil pathogen, and is also transmitted by the seed. The disease is most severe in light sandy soils such as those found in the Chitradurga region. The loss in yield due to crown rot at this stage is reported as being not very high, about 8–10%, because it tends to occur in patches<sup>7</sup>. However, during certain years, such as in 1994, the loss was as high as 30% in several fields of this region. The preventive measure is cheap, costing only about 10% of a typical loss (Table 1).

Leafminer *Aproaerama modicella*, Der. is a major pest in the southern and central parts of India. Leafminer attacks on the crop cause yellowing and webbing of the leaves and leaf drop, resulting in reduction in leaf area and considerable loss (Table 1). A dry spell any time between the 2nd week of August and first week of October can cause rapid multiplication of this pest. We see from Table 2 that the probability of a dry spell

Table 1. Cost-loss estimates for major pests/diseases

Disease/pest incidence	Cost of plant protection measure	Typical loss
Crown rot in seedling stage	Seed treatment by Dithane M-45 5 g/kg of groundnuts (40 kg seeds/acre) at Rs 36/acre	8-10%, i.e. Rs 320-400/acre
Late Tikka disease	Bavistein 1.5 g/l and 250 l/acre at Rs 345/acre	30-45%, i.e. Rs 1200-1800/acre
Leafminer in peg formation stage	Two sprays of Chloropyrephas at an interval of 15 days at 2 ml/l using 250 l/acre at Rs 750/acre	25-92%, i.e. Rs 1000-3600/acre

The estimate costs of the protection are based on the present prices of the chemicals and labour.

Typical yield is assumed to be 4 quintals per acre at Rs 1000 per quintal.

## CHITRADURGA WEEKLY RAINFALL DISTRIBUTION

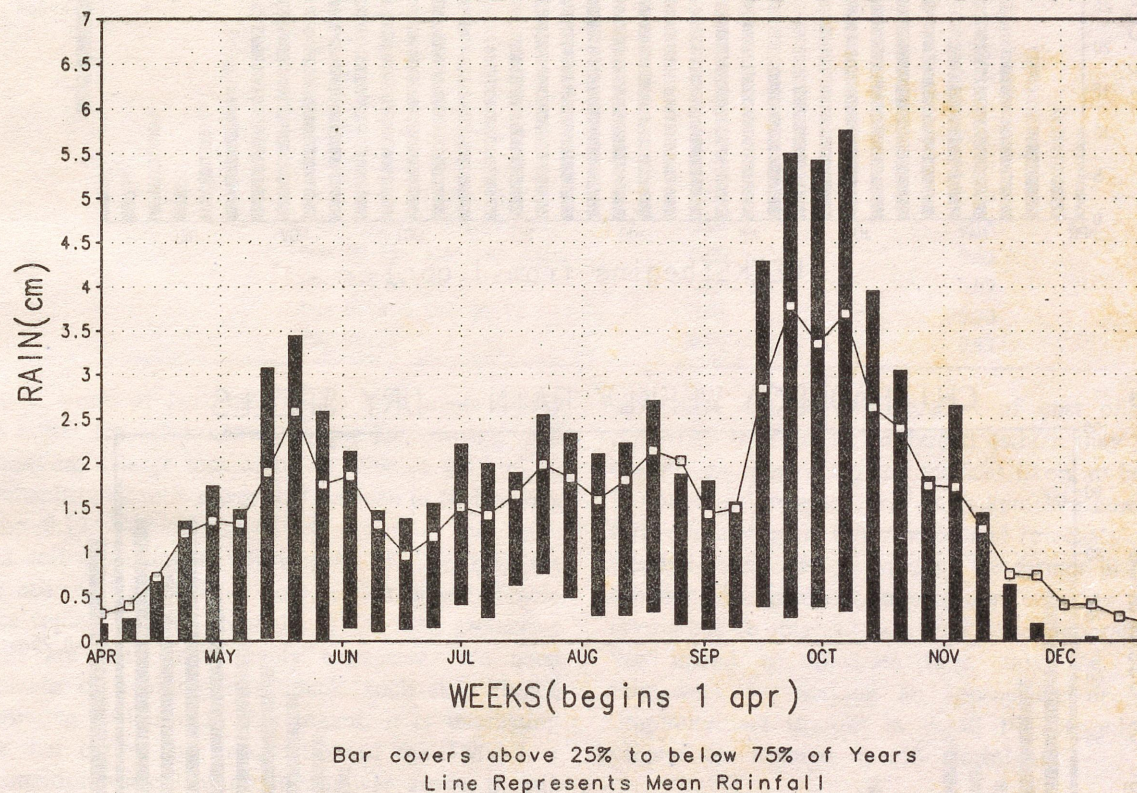


Figure 1. The mean weekly rainfall in cm at Chitradurga during April-December. For each week the range of variation from the minimum assured rainfall at 75% probability to the upper limit of rainfall (again for 75% of the years) is shown by a bar.

varies from 0.02 to 0.15 in this period, being maximum in late August and early September. The loss in yield is particularly high when the dry spell causes severe moisture stress<sup>8</sup>. If a wet spell occurs any time during the attack by leafminer, the population of the pest as well as the intensity of the attack decreases<sup>8</sup>. The costs of the remedial measure can be a large fraction, up to 25% of the loss (Table 1).

The occurrence of a wet spell during and after the

pod-filling stage, typically in the last two weeks of October (probability 0.21 from Table 2) promotes the incidence of the late Tikka disease<sup>9</sup>. The late Tikka disease is caused by *Cercospora personata*. The disease causes black pustules on leaves and stem, reduces the leaf area, affects pod-filling and decreases the quantity of straw available. The preventive measure involves considerable expenditure (Table 1).

A wet spell at the end of the pod-filling stage – first

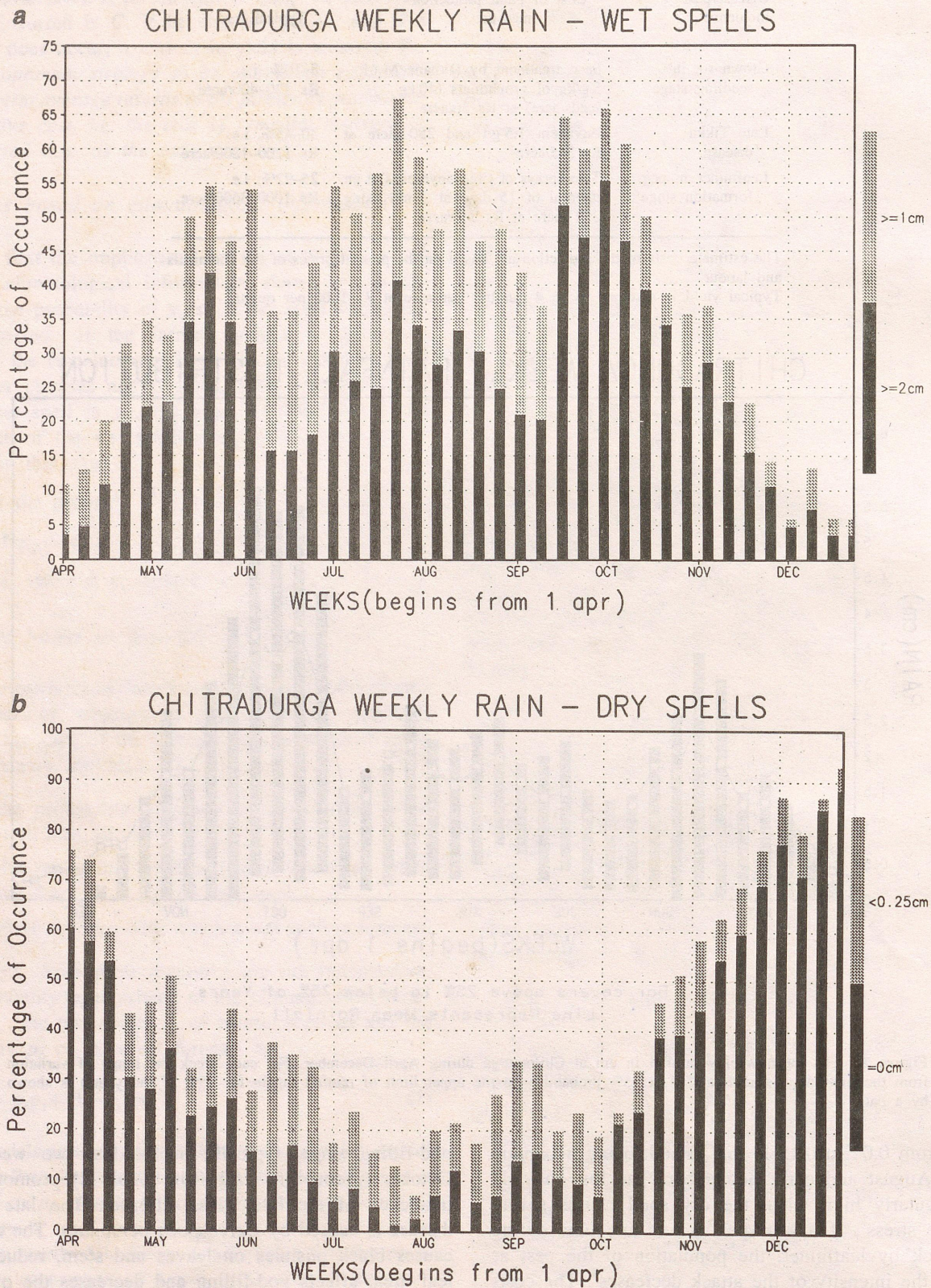


Figure 2. *a*, The probability of a wet week with rainfall greater than 1 cm (dotted) and 2 cm (solid). *b*, Dry week with rainfall less than 0.25 cm (dotted) or zero rainfall (solid) shown as a percentage for all weeks during April–December.

Table 2. Probabilities of wet and dry spells during different crop growth stages

Crop growth stages	Successive weeks	Probability of wet spell, i.e. > 2 cm rain per week for both weeks	Probability of dry spell, i.e. < 0.25 cm rain per week for both weeks
Sowing	Jul 1-7 to Jul 8-14	0.08	0.08
	Jul 8-14 to Jul 15-21	0.04	0.05
Seedling stage	Jul 15-21 to Jul 22-28	0.13	0.02
	Jul 22-28 to Jul 22-Aug 4	0.16	0.00
	Jul 29-Aug 4 to Aug 5-11	0.10	0.02
	Aug 5-11 to Aug 12-18	0.13	0.05
Flowering and peg formation stage	Aug 12-18 to Aug 19-25	0.10	0.05
	Aug 19-25 to Aug 26-Sep 1	0.09	0.05
	Aug 26-Sep 1 to Sep 2-8	0.10	0.15
	Sep 2-8 to Sep 9-15	0.08	0.10
	Sep 9-15 to Sep 16-22	0.10	0.05
Pod-filling stage	Sep 16-22 to Sep 23-29	0.31	0.06
	Sep 23-29 to Sep 30-Oct 6	0.23	0.02
	Sep 30-Oct 6 to Oct 7-13	0.30	0.07
	Oct 7-13 to Oct 14-20	0.17	0.10
	Oct 14-20 to Oct 21-27	0.21	0.23
	Oct 21-27 to Oct 28-Nov 3	0.11	0.27
Harvest	Oct 28-Nov 3 to Nov 4-10	0.08	0.36
	Nov 4-10 to Nov 11-17	0.13	0.47
	Nov 11-17 to Nov 18-24	0.06	0.49
	Nov 18-24 to Nov 25-Dec 1	0.04	0.55
	Nov 25-Dec 1 to Dec 2-8	0.00	0.66
	Dec 2-8 to Dec 9-15	0.00	0.69
	Dec 9-15 to Dec 16-22	0.00	0.70
Dec 16-22	0.00	0.83	

or second week of November – can lead to an attack of late collar rot (also known as pre-harvest peg, pod rot), implying a large loss of up to 35% of the yield<sup>10</sup>. The probability of such a wet spell is seen to be between 0.08 and 0.13. The control of the attack at this stage requires soil drenching by Dithane M-45. This involves a large cost of Rs 1300 per acre, which is comparable with the typical loss of about Rs 1400. The protective measures are thus prohibitively expensive. We need other means of avoiding this attack, such as a choice of alternative varieties. In this regard, it is interesting to note that before the introduction of the TMV-2, a longer-duration variety of groundnut was grown in this region. For this variety, the harvesting stage was later in the season when the probability of a wet spell is extremely low. It may be worthwhile to develop a variety for this region (which has a longer rainy season than Coimbatore from where the TMV-2 has been developed) which combines the advantages of the TMV-2 (a bunching variety) with those of a longer-duration variety (reduced susceptibility to collar rot).

An effective disease and pest management strategy implements appropriate plant protection measures before any significant damage is caused to the crop. However, decisions regarding taking up (or not taking up) such measures are taken by individual farmers. These decisions

are based on the consideration of cost of the plant protection measure to the farmer (which may vary from one farmer to another) and the loss likely to be incurred if mitigatory measures are not taken. We consider next how climatological information and forecasts of adverse weather events can be used by the farmer in taking the decisions. A practical prescription covering the entire season can be obtained only after more elaborate analysis. We intend to illustrate here only the theoretical framework for making an appropriate decision. For simplicity, we discuss in detail the procedure to be adopted for a single specific fortnight.

### Choice of strategies on the basis of climatological information and meteorological forecasts

We consider a simple case of choice between two alternative strategies – to adopt a remedial measure such as application of pesticides (at a cost  $C$ ) or not adopt it and suffer the loss  $L$  in productivity, if the adverse weather event (for example, a wet spell) occurs. The farmer has to decide whether to spray a pesticide or not on the basis of climatological information on the probability of a wet spell in the period of interest (e.g. probability of  $p_w$  of 0.16 for July 22 to August 4 from

Table 2), and a forecast of whether a wet spell will occur (if available). If he chooses to spray the pesticide, the cost incurred is  $C$ . If he chooses not to, and if a wet spell does occur, a loss  $L$ , in yield is incurred. We take the optimum strategy to be one which maximizes the long-term average returns to the farmer by minimizing the effective cost, i.e. the cost of remedial measure or the expected loss, as the case may be<sup>11,12</sup>.

#### Strategies based on climatological information

Consider first the implications for the strategies on the basis of climatological information alone, i.e. on the basis of the probability of  $p_w$  of a wet spell during the critical period. If the farmer decides to spray the pesticide, the cost incurred is  $C$ . On the other hand, if the farmer chooses not to spray, since the probability of the wet spell is  $p_w$ , the expected loss due to the occurrence of the wet spell is  $p_w L$ . Thus, the optimal strategy in this case is

spray the pesticide if  $C < p_w L$ ,

i.e. if  $p_w > C/L$ ,

do not spray if  $p_w < C/L$ .

#### Strategies based on forecast

While the methods of forecasting may be diverse (based on models of atmospheric circulation or statistical models), the skill of the forecast can be assessed using three summary statistics, viz.

$p_1$  – the probability of a wet spell occurring when it is forecast,

$p_0$  – the probability of a wet spell occurring when the forecast is for no wet spell,

$p_f$  – the frequency with which a wet spell is forecast.

However, these three measures are not independent. The probability  $p_f$  is related to the climatological probability  $p_w$ , the probability  $p_1$  of correct forecast and the probability  $p_0$  of incorrect forecast by

$$p_w = p_f p_1 + (1 - p_f) p_0. \quad (1)$$

For models generating an unbiased forecast, we expect a wet spell to be forecast on an average as often as it occurs, i.e.  $p_f$  should be equal to the climatological probability  $p_w$ .

For any worthwhile forecast, we expect that the probability of occurrence of a wet spell when a wet spell is forecast to be larger than that of the occurrence of the wet spell when no wet spell is forecast. Hence,

$$p_1 > p_0. \quad (2)$$

Combining (1) and (2) it can be shown that

$$p_1 > p_w > p_0. \quad (3)$$

This implies that a worthwhile forecast must be better than climatology, which is the traditional wisdom of meteorologists. How stringent the conditions on successful and unsuccessful forecasts are depends on the period. Thus, for a forecast of rainfall  $> 2$  cm during the first week of October, the probability  $p_1$  of such a wet week occurring when it is forecast must be greater than 0.55 (Figure 2a); the probability of a wet week occurring when no wet week is forecast,  $p_0$ , must be less than 0.55. The condition on  $p_1$  is less stringent for the first and second weeks of September, with only about 20% probability of rain of 2 cm or more. However, in that case the limit on  $p_0$  is more stringent, with an upper limit of 0.2.

Consider first the case when the forecast is for no wet spell. Then the wet spell occurs with the probability  $p_0$ , and if the pesticide is not sprayed, the expected deficit due to the incidence of pest is  $p_0 L$ . If the pesticide is sprayed, the expenditure is  $C$ . Hence, the returns will be maximized by choosing a strategy which minimizes the effective costs, i.e.  $\min(p_0 L, C)$ . If  $p_0 L > C$ , then spraying the pesticide will minimize the effective costs. On the other hand, if  $p_0 L < C$ , not spraying the pesticide will maximize the returns. The strategy recommended is thus

if  $p_0 < C/L$ : do not apply the pesticide,

if  $p_0 > C/L$ : apply the pesticide. (4)

Hence, if  $p_0 > C/L$ , even though the forecast is for no wet spell, the appropriate strategy is to spray the pesticide.

When a wet spell is forecast, analogously the expected loss is  $p_1 L$  and the cost of spraying the pesticide is  $C$ ; hence, the returns can be maximized by a strategy which implies  $\min(p_1 L, C)$ . The appropriate strategy is

if  $p_1 < C/L$ : do not apply the pesticide,

if  $p_1 > C/L$ : apply the pesticide. (5)

Thus, if the probability of a correct forecast is small ( $p_1 < C/L$ ), the strategy recommended is not to spray pesticide even though a wet spell is forecast.

Using (3) it is clear that  $p_1 < C/L$  implies  $p_w < C/L$ , and the strategy recommended by (5) for this case is the same as (1), which was obtained using climatological information alone. Similarly, from (2)  $p_0 > C/L$  implies  $p_w > C/L$ . The strategy recommended by (4) for this case is also identical to (1), which was obtained from climatological information alone. Thus, the use of forecast will yield a different strategy, only if

Table 3. Cost-loss ratios, appropriate strategies and minimum forecast skill

Pest/disease	Adverse weather event and critical period	$p_w$ (or $p_d$ )	$C$ (Rs/acre)	$L$ (Rs/acre)	$C/L$	Strategy: regarding protective measure	$E_c$ (Rs/acre)	$E^*$ (Rs/acre)	$p_0$	$p_1$
Crown rot	Wet spell July 22–Aug 4	0.16	36	320 400	0.11 0.09	Adopt	36	6	0.11 0.09	0.16
Leaf miner	Dry spell (1) in a specific fortnight between mid Aug to early Oct	0.02	750	1000 3600	0.75 0.21	Not adopt	20–72	15	0.005 0.015	0.75 0.21
		0.15					300 540	112	0.044 0.14	0.75 0.21
	(2) In any fortnight in the above period	0.4	750	1000	0.75	Not adopt	400	300	0.17	0.75
				3600	0.21	Adopt	750	300	0.21	0.4
Late Tikka	Wet spell last half of October	0.21	345	1200	0.29	Not adopt	252	72	0.17	0.29
				1800	0.19	Adopt	345		0.19	0.21

$p_w$  (or  $p_d$ ) Climatological probability of adverse weather event. (w = wet spell; d = dry spell).  
 $E_c$  Equivalent cost.  
 $E^*$  Equivalent cost for a strategy based on perfect forecast.  
 $p_0$  Upper limit on probability of wrong forecast.  
 $p_1$  Lower limit on probability of successful forecast.

$$p_0 < C/L < p_1 \tag{6}$$

For the forecast to have any impact at all on the decision between alternative strategies, the probability of a wet spell when no wet spell is forecast must be less than the cost-loss ratio, which in turn must be less than the probability of a wet spell when it is forecast.

For an unbiased forecast, the proportion of time a wet spell is forecast,  $p_f$ , must equal the climatological probability  $p_w$ . Note that the upper limit of  $p_0$  is determined by (3) and (6). When  $p_f$  equals  $p_w$ , it can be shown that (1), (3) and (6) imply

$$p_0 < \frac{p_w}{1-p_w} \left(1 - \frac{C}{L}\right) \text{ for } p_w < C/L,$$

$$p_0 < C/L, \text{ for } p_w > C/L. \tag{7}$$

The corresponding lower limits on the probability of successful forecasts  $p_1$  are simply that  $p_1$  be larger than the largest of  $p_w$  and  $C/L$ . As pointed out earlier, the limits on  $p_0$  and  $p_1$  are not independent. However, we have specified both so that it is easy to assess which of them is more stringent in a given case.

Value of forecast

For  $p_0$  and  $p_1$  obeying (6), equations (4) and (5) imply that pesticide should only be applied when a wet spell is forecast and not when a wet spell is not forecast.

The expected effective cost in that case will be

$$E = (1 - p_f) p_0 L + p_f C.$$

Note that the loss in yield occurs only with probability  $p_0$  of the wet spell occurring when no wet spell is forecast. Consequently, the effective cost increases with increasing  $p_0$ , or decreasing  $p_1$ . The effective cost for an unbiased forecast ( $p_f = p_w$ ) is given by

$$E = (1 - p_w) p_0 L + p_w C. \tag{8}$$

For a perfect forecast ( $p_1 = 1, p_0 = 0$ ) the above equation reduces to

$$E^* = p_w C. \tag{9}$$

If the strategy were chosen on the basis of climatological information alone, the expected effective cost,  $E_c$ , is

$$E_c = p_w L \text{ for } p_w < C/L,$$

$$= C \text{ for } p_w > C/L. \tag{10}$$

The value of the forecast,  $V$ , can be defined as the difference between the effective cost  $E$  and the effective cost  $E_c$ , viz.

$$V = E_c - E.$$

Using (7) and (10) we get

$$V = L(1 - p_w)(C/L - p_0) \text{ for } C/L < p_w,$$

$$= L(p_w - p_0(1 - p_w) - p_w C/L) \text{ for } C/L > p_w. \tag{11}$$

It can be seen that for any  $C$  and  $L$ , the value  $V$

## RESEARCH ARTICLES

increases as  $p_0$  decreases (i.e.  $p_1$  increases). For a given  $p_1$ , the value increases with  $C/L$  until  $C/L$  equals the climatological probability  $p_w$  and decreases for further increases in  $C/L$ .

### Implications for the case of groundnut

We consider here the implications of the above analysis for the choice of strategies for combating the three pests/diseases discussed earlier in rainfed groundnut. On the basis of the typical costs, losses for each pest/disease (Table 1) and the climatological probabilities of the adverse weather event in the critical periods, the strategy to be adopted when only climatological information is available as well as the limits on the skill of the forecast are given in Table 3.

Note that when a forecast of skill high enough to have an impact on strategy (i.e. when (3) and (6) are satisfied) is available, the strategy is to adopt the protective measure when an adverse event is forecast and not adopt it when it is not forecast. The critical periods mentioned in Table 2 are based on the assumption that sowing is done in the second week of July. Depending on the actual time of sowing in a given season, these periods may shift a little. In that event the value of the climatological probabilities of the adverse weather events have to be revised using Table 1.

The first case considered is of crown rot due to a wet spell occurring 2–3 weeks after sowing. As the climatological probability of the wet spell,  $p_w$ , during the critical period is higher than the cost-loss ratio, if only climatological information were available then the strategy should be to adopt the protective measure. The protective measure is cheap, being less than 1% of the returns. Although the equivalent cost may be reduced considerably by using a forecast, this gain is not much in terms of the money saved. Also, the condition on the probability of wrong forecast is so stringent that when the forecast is for no wet spell, the probability of a wet spell occurring,  $p_0$ , should be less than 9%. This is a case when the strategy based on climatological information is adequate; the condition on the allowable error in forecast is too stringent and returns too low to make the forecasting worthwhile.

Consider next the case of the leafminer attack, which is favoured by the occurrence of a dry spell any time between August and October. The probabilities of such a spell occurring in a specific fortnight in this period range from 0.02 to 0.15 (Table 2). We consider the strategies for the two limits of this range of  $p_w$  in Table 3. Here the entire range of cost-loss ratios is above that of the climatological probabilities  $p_w$  and the strategy based on climatological information alone is not to adopt the protective measure. Again, while the returns are greater if forecasts are used, the allowable limit for

wrong forecasts, i.e. for  $p_0$ , is perhaps far too stringent to make skillful forecasts which can have a significant impact. We note, however, that in these cases, although on an average the farmer's returns are maximized by adopting the optimum strategy, when an intense attack occurs the losses suffered are high. In such situations, a strategy which minimizes the maximum losses (minimax) may be more appropriate. However, in this paper we restrict our attention to determining strategies that maximize the average returns and leave alternative optimization to future studies.

There is another important point about a leafminer attack. Although the probabilities for a dry spell within a specific fortnight during August–October range from 0.02 to 0.15, we find the probability of at least one such dry spell during this period to be 0.40, which is high. Thus, the average loss expected if no protective measure is adopted is high; the impact of a skillful forecast of a dry spell—perhaps based on conditional statistics, i.e. using the rainfall profile in the season up to that point, would be more than that assessed in Table 2.

In the case of late Tikka, depending upon the cost-loss ratio, the strategy based on climatological information changes from one in which the protective measure is not adopted to one in which it is. Since  $C/L$  varies from values less than  $p_w$  to values in excess of  $p_w$ , the value of the forecast is very high in this case. If a forecast of sufficient skill can be generated, the returns to the farmer can increase substantially as the losses are high.

We find, therefore, that a significant impact on productivity of groundnut is possible by forecasts of the wet spell during the critical period for the late Tikka disease. If reliable forecasts for a dry spell in the fortnight ahead, during August–October, are available, then considerable loss due to a leafminer attack could be avoided. On the other hand, forecasts are not likely to have any impact for prevention of crown rot.

### Summary and conclusions

We have attempted to show how the nature of the forecast required, and the minimum skill of the forecast, depends upon the agricultural system, using the example of rainfed groundnut in semi-arid parts of Karnataka. We find that for certain purposes (e.g. combating crown rot at seedling stage), climatological information on the variability of the adverse weather events may be adequate; forecast is unlikely to have a significant impact. But for others (such as late Tikka) substantial loss can be prevented if forecasts of adequate skill are available. An analysis of cost-loss ratio and the minimum skill of forecast can also point out cases (such as avoidance of collar rot at pod-filling stage) where neither

climatological information nor forecasting is likely to be useful. For such cases, alternative varieties or cropping patterns, better suited to the climatic pattern, may have to be adopted or developed.

A detailed analysis of every cropping system which is sensitive to fluctuations in climate is required for identification of the nature of those weather/climate events which have a large impact on productivity. To assess the impact of dry spells more realistically, the studies will need to incorporate realistic hydrological models which yield soil moisture as a function of the climate variables and detailed crop physiological models. This will require concerted efforts by genuinely interdisciplinary groups.

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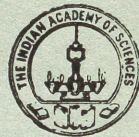
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## BOOK REVIEW

### Mathematical Evolutionary Theory

Edited by MARCUS W. FELDMAN; Princeton University Press, Princeton, 1989; 341 pages

As the dedication of the book points out, this collection of articles was brought out to celebrate Prof. Samuel Karlin's contributions to mathematical evolutionary theory. In keeping with the broad scope of Karlin's research interests, this volume goes far beyond mathematical evolutionary theory, to include topics as diverse as the behaviour, ecology and sexual selection in ladybird beetles and the cultural transmission of milk use. The presentation also ranges from the pure, rigorous, theorem-proving variety, through moderate to liberal use of numerical simulations and analysis of field data, to almost completely descriptive narration.

Prof. Marcus Feldman has not only put together a stimulating collection of articles (besides contributing a couple of them himself), but has thoughtfully arranged them in a logical sequence. The book is divided into two sections: stochastic and deterministic models the first one; and behaviour, ecology and evolutionary genetics the second.

The first section begins with a contribution by Warren J. Ewens, on the effective population sizes in the presence of catastrophes—one of the relatively recent subjects to attract theoreticians is conservation biology. Faced with rapidly dwindling populations of endangered animals on one hand, and severe resource and logistic constraints on the other, the question of estimating the minimum viable population size for a given species has assumed critical importance. The impossibility of including all the myriad complexities one encounters in a real-life situation has forced modellers into using a mathematical idealization—the effective population size of a population. The long-time trends for a real population turn out to be close to the ones predicted from the dynamics of a population of hypothetical organisms, with highly simplified life histories and population structures, and population size equal to the effective population size of the real population. Unfortunately, as Ewens's incisive analysis points out, the estimate of the effective population size turns out to be quite different depending on the specific long-term trends one is interested in, e.g. rate of loss of genetic variability, and the specific features of the real population that are of relevance, e.g. geographical fragmentation. Ewens further investigates the impact of catastrophes, which can completely wipe out some local populations of species. Using theoretical arguments as well as numerical computations, he not only demolishes some of the earlier conjectures but obtains several new results. Written in a lucid manner with frequent references to Sam Karlin, Ewens's article ends by posing a series of important questions emerging from the present work, which should keep several theoreticians busy for quite a while.

The next contribution, by Geoffrey A. Watterson, examines how genetic diversity of a population is affected when the population undergoes a series of

bottlenecks—episodes in history where the population size is reduced to a relatively low value. A detailed theoretical analysis is augmented with numerical simulations of a simple situation where a population cycles between large and small sizes. In addition to providing estimates of homozygosity, Watterson also answers an intriguing question: How ancient would the most ancient allele be in a sample from such a population?

The highly mathematical and esoteric contribution by Simon Tavoré, among other aspects, raises the next obvious question: How many copies of such an allele would be present? Tavoré extends the earlier work of Karlin and McGregor on stochastic fluctuations in the sizes of families, based on the birth–death–immigration process, to include the order of appearance of ‘new’ families. Since the mathematical formalism describing the dynamics of families, alleles or species is the same for these processes, Tavoré’s results are also pertinent for estimating the fraction of the total population contributed by the oldest species.

John H. Gillespie has come up with a characteristically incisive and provocative article, ‘When not to use diffusion processes in population genetics’. The diffusion approximation trades ‘accuracy for tractability by approximating the dynamics of discrete time stochastic processes with continuous time diffusion processes’. Changes in gene frequencies in population depend on several concurrently acting forces, such as mutation and selection. The diffusion approximation, which requires all these forces to be of the same order of magnitude, is clearly inadequate when multiple influences are at work. Despite the statement that he wants only to call attention to the problems and not to provide solutions, Gillespie does provide some guidelines. To model molecular evolution, he describes a set of algorithms such that the number of iterations needed for an algorithm to come to termination is formally equivalent to the number of alleles going to fixation. The article also discusses fluctuating fitnesses, and the results of the simulations presented there bring out the differences between the diffusion processes rather dramatically. Written in a refreshingly original style, this paper will amuse some (‘This section is presented as a challenge to occupy Sam Karlin until his 70th birthday volume’), stimulate many (by the various open problems posed in the text), and raise not only eyebrows but the hackles of a few (‘the pre-eminent position of the neutral allele theory as an explanation for molecular evolution may be due more to the simplicity of its mathematics than to its biological underpinnings’).

The next three articles are devoted to phenomena involving multiple loci. When the recombination frequency is low, and when populations that differ in gene frequencies are allowed to mix, the genotypic frequencies of the resulting population may show departures from what one expects them to be based on gene frequencies. Karlin and Feldman had earlier investigated this phenomenon of linkage disequilibrium, which generally leads to an excess of homozygotes, for a two-locus model. Freddy B. Christiansen describes a natural generalization to cover multiple loci, and provides explicit solutions for situations involving up to nine loci. The next article by Bruce S. Weir and C. Clark Cockerham is as thorough as its title, ‘Complete characterization of disequilibrium at two loci’. Weir and Cockerham provide expressions not only for the maximum likelihood estimates for the various disequilibrium measures, but for the sampling variances as well. These promise to be very useful in testing hypotheses based on genotypic data. Weir and Cockerham

have also carried out a large number of simulations to validate their formulae. A lucid description of why (and when) a detailed statistical analysis along the lines suggested by them should be routinely carried out for genetic data is also given. An interesting sidelight of their contribution is the use of the software package MACSYMA for carrying out the extremely elaborate algebraic manipulations involved in trigenetic and quadrigenic disequilibria.

Uri Liberman and M. W. Feldman (with some assistance from K. E. Holsinger) present an even more complete analysis of a two-locus model describing the evolution of migration rates. They consider two populations, each favouring a different allele at the first locus. The second locus governs the rate of migration between the two populations. After a concise but clear statement of the assumptions and notations in the model follow pages and pages of algebra, spelling out each and every term, successively describing the dynamics of gene frequencies, existence of equilibrium, external stability, internal stability, and so on. The discussion section explains in simple terms what the conclusions are (zero migration rates are generally preferred), and also why they are contrary to biological reality. Perhaps the most interesting finding emerging from this model is a set of reasonable parameter values that lead to cyclical changes in gene frequencies, a rarity in standard population-genetic models. The numerical analysis presented in the appendix is indeed a *tour de force*, uncovering cycles with periods as large as 155,276 generations.

The second section of the book opens with another important contribution, from Feldman and Luigi L. Cavalli-Sforza, which describes how the process of evolution operates under the joint influence of genetic and cultural factors. Traditionally, in population-genetic models, the phenotype is assumed to be determined by genotype. Many behavioural phenotypes, however, can often be acquired culturally—by learning from conspecifics. Cultural transmission, unlike genetic transmission, can occur via a rich set of pathways—horizontal (between individuals of similar ages), oblique (from older, non-parent individuals), and so on. The rate of spread of a trait by cultural transmission can be orders of magnitude higher than by the genetic route. Feldman and Cavalli-Sforza, who have pioneered research in this area, present an extremely thorough analysis of a two-allele two-phenotype model, and use the results to obtain insights into the (cultural) spread of the practice of dairying in a genetically heterogeneous population where one genotype can absorb lactose (and thus can derive advantage from using milk) while the other cannot (and is adversely affected by milk). In what may be an epitome of a systematic, step-by-step approach, they grind the asexual-haploid model, follow it up with the sexual-haploid model, and (skipping the asexual-diploid model) finally reach the sexual-diploid model. At each step, conditions (relations between the parameters of the model such as the transmission rates, advantage/disadvantage due to milk usage) necessary for the initial increase of the novel trait (or allele) are derived wherever possible; detailed numerical investigations are presented otherwise. The question of interest is whether the genetic trait of the ability to utilize milk, and the cultural trait of practising dairying, will increase sufficiently in three-hundred-odd generations for realistic values of the parameters. The rather interesting answer highlights the role of 'history'. If lactose absorbers were not very rare to start with, then even for moderate values of selective advantage, they can obtain substantially high frequency; but if they were rare, unrealistically high values of selective advantage are needed

to achieve the same. Feldman and Cavalli-Sforza's article, by its clarity of exposition and novelty of ideas, is likely to be very successful in culturally transmitting the trait of working on gene-culture coevolution to mathematical evolutionary biologists.

Perhaps the most important advance in evolutionary theory in the latter half of the present century is Hamilton's theory of kin selection. Hamilton showed that altruistic behaviour (which involves some fitness cost to the performer and results in some fitness benefit to the recipient of the act) can be selected if it is more likely to be performed towards genetically related individuals. Hamilton's rule is a succinct quantitative statement: a trait will spread if the ratio of benefit to cost is greater than the coefficient of relatedness between the two individuals involved in the act. This rule is the cornerstone of most of the contemporary research in evolutionary biology, especially that concerning evolution of social behaviour. Marcy K. Uyenoyama presents a particularly novel extension of this rule to multilocus situations. She considers two-locus models, subjected to recombination and epistatic interactions (effect of an allele at one locus on the expression at another locus), and attempts to define relatedness in such a way that Hamilton's rule is valid. Suffice here to say that she is successful in doing so, rather elegantly. The article is impressively rigorous, and the model system chosen for exploration (brother-brother and sister-sister altruism in haplodiploids—groups such as bees, wasps and ants, which include highly social species) could not have been more appropriate. Members of the esoteric group of pure evolutionary theorists would no doubt greatly appreciate the contribution.

The other important field opened up by Hamilton is sex-ratio theory. In its simplest form, it predicts how many daughters and sons an individual should produce, i.e. the choice of optimal allocation of resources between male and female offspring. What is optimal, however, also depends on what the rest of the individuals in the population do; and a game-theoretic analysis leads to the evolutionarily stable strategy (ESS). A population where resource allocation is according to the ESS is stable against invasion by a mutant. That is, the resource allocation at ESS is the best possible in the sense that no better strategy exists. Sabin Lessard analyses more intricate details of this situation: Is there any quantity that is maximized? Does it increase monotonically? At what rate are non-ESS mutants eliminated?... The study is very comprehensive, includes analytical results as well as numerical simulations, encompasses a range of combinations of male and female fitness functions, and discusses a variety of extensions of the original model (e.g. partial selfing, variable environment, sex-linked traits). The general result is that evolution maximizes the product of male and female fitnesses (or some very closely related functions of these). Occasional decrease from one equilibrium to another is however seen in some of the simulations, highlighting possible departures from monotonicity.

The next article of the collection is a study on mating preferences in ladybird beetles by Peter O'Donald and Michael E. N. Majerus. While it is the fittest that is selected during the course of evolution, one can become fittest in a number of different ways—for example by being extremely attractive to the opposite sex. The peacock's tail is the most celebrated example of this phenomenon of sexual selection. Ladybird beetles are a particularly fascinating system to work with because of the wide range of patterns seen on them—from two light spots on a dark background through many intermediate stages to two dark spots on a light background. Following

from Karlin and O'Donald's earlier work, O'Donald and Majerus first theoretically investigate how the frequency of different melanics (different types of dark patterns) changes in the population when females mate preferentially with some of these forms. They follow it up with very interesting experimental work involving quantification of the preference in mate choice by females, what pattern a female prefers being determined by the genotype of the female. The experimental results rule out the runaway selection model that predicts the preponderance of the dark form. The inclusive preference model, developed by the authors in collaboration with Karlin, however, turns out to be consistent with the experiments.

If one is to single out only one article that illustrates not only what mathematical evolutionary theory is all about, but also how it should be practised, and does so in a lucid and logical manner satisfactory to mathematicians and accessible to non-mathematicians, the contribution by Jonathan Roughgarden on marine life-history strategies is an automatic choice (and perhaps not only from among those in this book). Marine organisms show a wide diversity of forms—from purely benthic (rooted to a spot) to purely pelagic (free-swimming) via a range of biphasic types where one life stage (usually larval) is pelagic while the other is benthic. Why should this be so? What factors dictate the particular choice of life-history strategy? These are the kinds of questions raised by Roughgarden. The advantages of the pelagic state are wider dispersal and perhaps a better chance of obtaining food, the disadvantage is the higher mortality rate; the situation is the exact opposite for benthic forms. Roughgarden presents a complete model covering the entire life cycle of biphasic organisms which includes the above factors, and obtains the combinations of values of parameters (and even functional forms) that lead to purely benthic, purely pelagic or mixed strategies. Two of the most pleasing outcomes of the model are the prediction of conditions that lead to the evolution of colonial life forms and an answer to the question of why marine plants are rarely biphasic. The latter has to do with the way a plant grows—exponentially and not according to a power law! It is very rarely that a comprehensive but transparent model can be formulated, leading to insights into such profound questions in so elegant a manner. The discussion (titled 'The major questions re-examined') is even more readable, and contains many interesting empirical facts—prevalence of toxic sponges in the tropics, for example. The conclusions ('Some final conjectures') draw interesting parallels between marine and terrestrial life forms and hint at why birds and animals displaced dinosaurs. Definitely an article not to be missed!

The next article, by Norman L. Kaplan and Richard R. Hudson, looks at the evolution of highly repeated DNA sequences interspersed within genomes. Mammalian DNA contains many families of such sequences whose function is not yet clear: epithets like 'junk DNA' and 'selfish DNA' have been used to describe them. A copy of such a sequence is capable of replicating itself more than once, thereby increasing its copy number in the host genome; the opposite process of self-excision is also possible. While earlier models assumed each copy to be capable of replication, Kaplan and Hudson assume (with some justification) that only one copy of the set is able to do so. The rest of the copies, being subject to mutations, begin to differ from each other over a course of time. Kaplan and Hudson work out, among other aspects, the time of divergence between two copies on the basis of similarity of their sequences. They then use the data on the sequence of the *Alu* repeat sequence

family in both human and chimpanzee DNA to estimate the parameters of the model (the mutation rate, the excision rate, and so on). Finally, these values are used to predict the extent of similarity between the sequences of the *Alu* family in humans and galagos. Not only are the predictions in agreement with the data, but the estimated parameter values are biologically realistic; the Kaplan-Hudson model is thus validated.

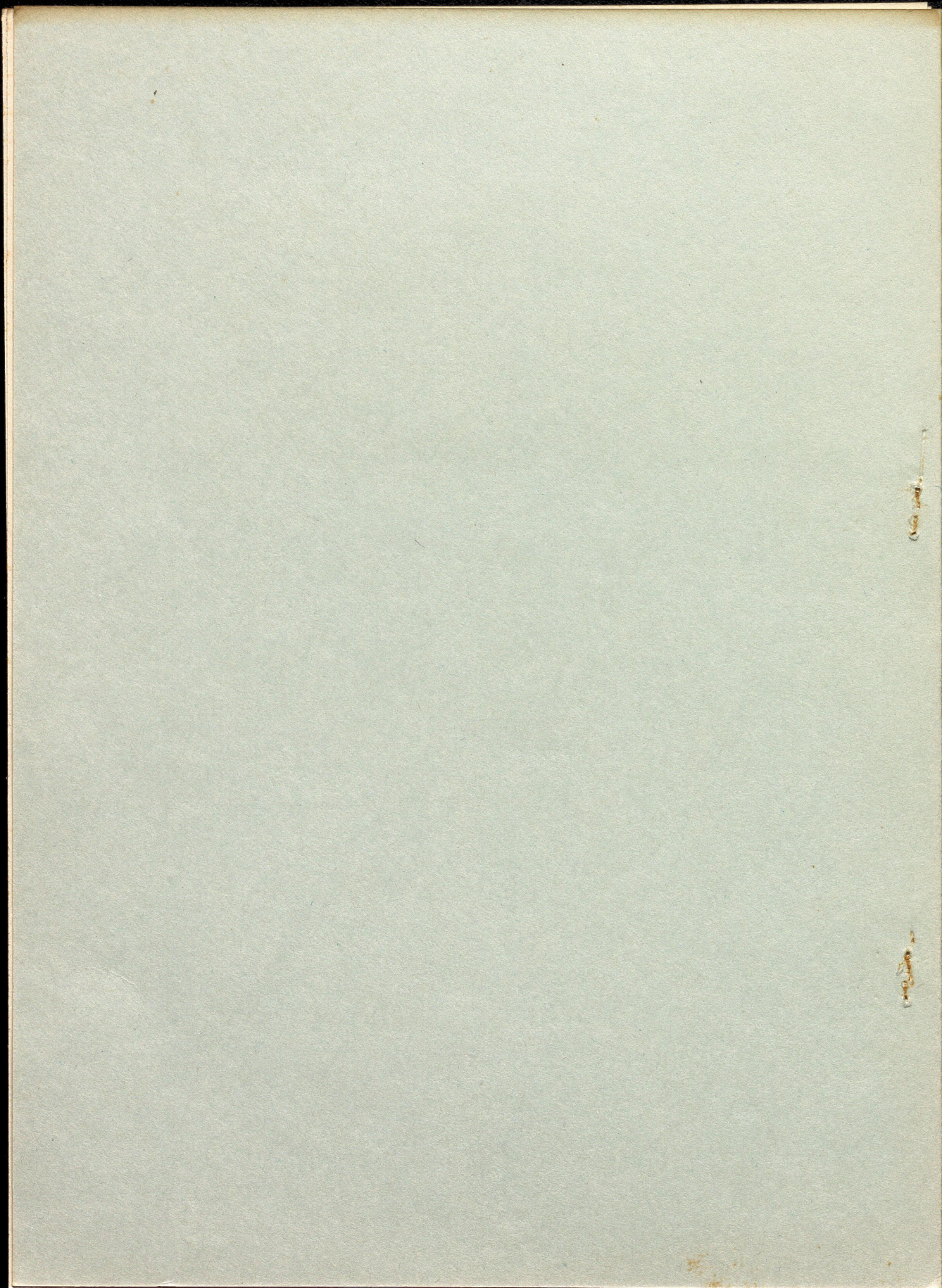
Ironically, the only completely non-mathematical and almost totally descriptive contribution is by Walter F. and Julia G. Bodmer, who, together with Samuel Karlin, founded the mathematical biology program at Stanford University. It describes at length the HLA system, corresponding to the major histocompatibility locus, probably one of the most polymorphic of the known human loci. Study of this system received a major boost when organ transplantation became more common. When donor and recipient have similar alleles at this locus, a transplant is more likely to succeed; differences lead to a strong immune response that leads to rejection of the transplant. Detailed tissue-type-matching studies, which screen a large number of potential donors to select the most suitable one, have generated a wealth of genetic data for the HLA system. The Bodmers describe the extent of international cooperation and organization involved in HLA research, and give a glimpse of the complexity of the system. They highlight the wide differences observed in the genetic composition of different human populations observed worldwide, and suggest that natural selection might have been responsible for these. Another reason why the study of the HLA systems has assumed importance is the fact that certain combinations of alleles make the individual strikingly more susceptible to certain diseases. The physiological basis and the evolutionary significance of these effects are unknown. (Why should nature evolve mechanisms for rejecting transplants? It is not very easy to imagine transplantation being a natural phenomenon.) The Bodmers point out the novel processes (gene conversion, gene duplication) that are likely to have played an important role in the evolution of the HLA system, and indicate that new population-genetic models need to be explored to meet the challenge of making sense of the data on genetic variability available now at the molecular level. What the article lacks in clarity is more than compensated by this fitting finale to the book—showing the direction for future research, where the models and techniques pioneered by Samuel Karlin promise to lead to results of great practical (clinical) and theoretical (evolutionary) interest.

Each of the two sections of the book is preceded by a summary that gives an overview of the salient features of each contribution. This is a particularly attractive feature (not merely for reviewing the book) for the non-mathematical biologists (who abound in nature), who may thereby be able to grasp the important results presented here. The collection covers almost all the contemporary evolutionary issues (evolution of sex is a notable omission). The variability of presentations is rather striking—from the 'by the theoretician, for the theoretician' type that no biologist can hope to understand (exemplified by the contribution by Christiansen) to the one by the Bodmers which will delight all (molecular) biologists and stump all mathematicians (except possibly Samuel Karlin). As a consequence, while almost no one will find the book uniformly comprehensible, almost every evolutionary biologist will have something to gain from it.

In summary, a most useful reference book, to know both the kinds of work that have been (and are) done in mathematical evolutionary theory, and, more importantly, the kinds of unsolved problems that can (and should) be investigated. In the five years since its publication, many of the topics covered in this book have been investigated in more detail (and Prof. Karlin has been as active as ever, making many important contributions in the field of DNA sequence analysis). However, students, teachers, and researchers of evolution in general and mathematical evolutionary theory in particular would continue to find this book stimulating.

N. V. JOSHI

Centre for Ecological Sciences  
Indian Institute of Science  
Bangalore 560 012



# Impact of human extraction on tropical humid forests in the Western Ghats in Uttara Kannada, South India

R. J. R. DANIELS\*, MADHAV GADGIL\*\* and N. V. JOSHI†

\* M.S. Swaminathan Research Foundation, 3rd Cross Street, Institutional Area, Taramani, Madras 600113, India;

† Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, Karnataka, India; and

\*\* Biodiversity Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur, Bangalore 560064, Karnataka, India

## Summary

1. Thirty strip transects of 2400 m<sup>2</sup> each, in the evergreen forest tract of the district of Uttara Kannada in South India, were clustered into two groups with high and low levels of disturbance on the basis of the density of perennial flowering plants and the fraction of deciduous species.

2. The set of 20 transects corresponding to low disturbance localities harboured  $48 \pm 6$  (mean  $\pm$  SD) species and  $694 \pm 135$  individuals per transect, while the other 10 transects affected by high levels of disturbance supported  $36 \pm 12$  species and  $379 \pm 135$  individuals.

3. Eighty-four of the total of 200 species (operational taxonomic units) were exclusive to sites of low disturbance, and 28 to those of high disturbance; 88 species were shared by sites of high and low disturbance. This number of shared species was significantly less than expected on the basis of chance alone.

4. The differences in species richness, as well as those in species turnover ( $0.73 \pm 0.07$  for high and  $0.65 \pm 0.01$  for low disturbance sites) were significant at the 1% level, but were as expected given the lower plant densities at sites of high disturbance.

5. Lack of coppicing ability in conjunction with their use in the plywood/matchwood industry has led to the disappearance of several evergreen species such as *Syzygium gardneri* and *Myristica malabarica* at sites with high levels of disturbance.

6. With villagers concentrating on harvests of trees in the height class of 4–8 m as poles, and commercial interests mostly extracting trees > 16 m in height, there was a reduction of around 45% across all height classes between sites of low and high levels of disturbance.

**Key-words:** biodiversity, hot spot, human cultural disturbance, plywood industry, species turnover.

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## Introduction

Tropical humid forests are amongst the most diverse, most productive and most threatened of biological communities. Indeed 14 of the 18 biodiversity hot spots identified by Myers (1988, 1990) represent this biome. Two of these, the Eastern Himalayas and the Western Ghats, occur in India. The Western Ghats constitute a hill chain of length 1600 km and, along with the narrow coastal strip, form a region with an average width of 105 km, and receiving annual rainfall in the range of 2000 to 6000 mm, largely concentrated in the monsoon months of June to October. This region can potentially support 64 750 km<sup>2</sup> of evergreen forests and 103 000 km<sup>2</sup> of deciduous forest.

On the basis of satellite imagery and vegetation maps available in the mid 1980s, Gadgil & Meher-Homji (1986) estimated that the evergreen forest cover had been reduced to 22 000 km<sup>2</sup>. The Ministry of Environment and Forests

(1989, 1992), of the Government of India, estimated a 20% reduction in forest cover from the Western Ghats states of Kerala, Tamil Nadu, Karnataka, Goa and Maharashtra between 1972 and 1982, and a lower rate of 4.32% between 1982 and 1990. This was subsequently brought under check, leading to an actual increase of 0.01% between 1991 and 1993 (Ministry of Environment and Forests 1993).

While the process of loss of forest cover in the Western Ghats has thus been contained, pressures leading to erosion of forest biomass and local extinctions of species continue (Pascal 1988; Gadgil & Subash Chandran 1989b; Nadkarni, Pasha & Prabhakar 1989). The present investigation attempts to document these changes on the basis of a set of 30 strip transects sampled in the single most extensive remaining tract of the Western Ghats evergreen forest, in the district of Uttara Kannada (13°55'–15°32'N and 74°05'–75°05'E). Geologically, this is a region of

transition between the northern Deccan traps and the southern Archaean crystalline shield, with a very narrow coastal strip and low broad hills rising to no more than 1000 m before merging with the Peninsular Plateau at an altitude of 600 m. Champion & Seth (1968) characterized the vegetation of this tract as west coast evergreen/semi-evergreen forest. Pascal (1982, 1984) has published maps (at 1 : 250 000) of the vegetation of the district, which is characterized as belonging to the *Memecylon-Syzigium-Actinodaphne* and *Persea-Diospyros-Holigarna* series of tropical wet evergreen forest. The vegetation is distributed in five broad zones governed by the rainfall gradient, and remains most intact in the northern and southern evergreen zones (Fig. 1). Even here the vegetation is an intricate mosaic of different stages of degradation. There has been little extraction from the more inaccessible slopes in these two zones, although many of these areas might have been under shifting cultivation prior to 1865 (Gadgil & Subash Chandran 1989b). This tract thus provides an excellent setting for comparing forests under varying degrees of human impact.

These forests have been and are still subject to a variety of human impacts, including commercial logging, extraction of fuelwood and fencing poles, lopping of leaves, cattle grazing and dry-season fires. Little quantitative information is available on any of these activities, so that it is not possible to grade different localities along a well-defined scale of disturbance. It is, however, reasonable to assume that increasing levels of disturbance are accompanied by a reduction in forest biomass, an opening of the forest canopy and a reduction in soil moisture. These environmental changes favour deciduous species at the cost of shade-tolerant and moisture-loving evergreen species (Puri *et al.* 1983; Pasal 1988). The extent of reduction in forest biomass and increase in the fraction of deciduous species may then serve as useful measures of increasing levels of disturbance for the evergreen forest tracts in the Western Ghats. We discuss below the changes in forest composition in terms of species richness, species turnover, attributes of constituent species and the structure of the vegetation along such a gradient.

### Materials and methods

The study was based on 30 transects of 600 × 4 m, i.e. 2400 m<sup>2</sup>, selected in order represent all levels of degradation of the evergreen forest vegetation in the Uttara Kannada district, as indicated on Pascal's (1982, 1984) vegetation maps at a scale of 1 : 250 000 (Table 1). Along the transects we sampled all flowering plants excluding grasses, epiphytes, seedlings at cotyledon stage and shorter herbaceous plants. Herbaceous plants over 1 m in height belonging to the families Zinziberaceae and Marantaceae were included. The plants were assigned to seven height classes, namely 0-1, 1-2, 2-4, 4-8, 8-16, 16-32 and >32 m (Daniels 1989; Daniels, Joshi & Gadgil 1992). In all 200 species were involved; of these 121 could be identified to species level, 35 only to genus level, and nine only to family level, with the help of Saldanha's collec-

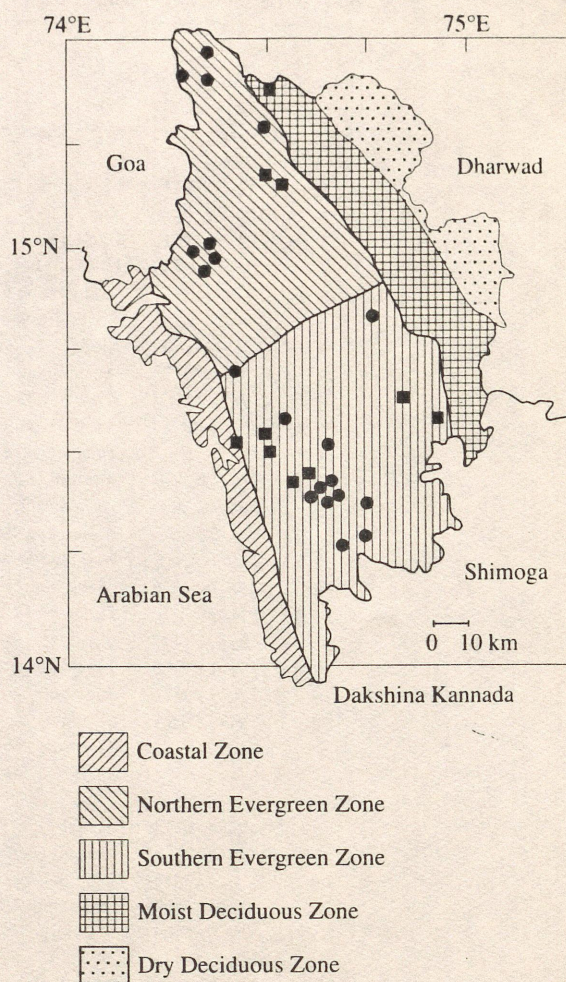


Fig. 1. Vegetation zones in Uttara Kannada with locations of sites with low (●) and high (■) levels of disturbance.

tions lodged at the Indian Institute of Science (Saldanha & Nicholson 1978; Saldanha 1983). The remaining 35 were considered to be operational taxonomic units (OTUs) with the rank of species.

The 165 securely identified OTUs were then characterized in terms of evergreen or deciduous habit, incidence of spines, thorns or latex, sun-loving or shade-loving habit, and pioneer, climax or relict species status (Pascal 1988). Our own field observations were used to assess the coppicing abilities of various species and their involvement in a variety of human usages. Records of the Forest Department provided additional information on commercial uses, especially in the plywood and matchwood industry (Gadgil & Subash Chandran 1989a).

The composition of the 30 sampled plant communities was then plotted in the space defined by two indicators of disturbance, namely plant density and fraction of individuals of deciduous species (Fig. 2). The 30 points seem to constitute two distinct clusters in this space. As Fig. 1 indicates, sites assigned to the two clusters were geographically interspersed and did not represent distinct bioclimatic zones. Rather, they probably correspond to categories of low and high levels of disturbance. It is therefore of interest to assess whether these were significantly distinctive in their species composition. The frequency distribution

Table 1. Details of the 30 sample localities

Number. latitude and longitude	Locality	Altitudinal range (m)	Date of sampling	Vegetation series*	Incidence of trails	Incidence of induced fire	Incidence of grazing
Low disturbance							
1 14°15'N-74°38'E	Mastimane	60-200	4-4-87	PDH	-	-	-
2 14°36'N-74°33'E	Yan	~140	29-4-87	PDH	+	-	Seasonal
3 14°31'N-74°38'E	Bandal Ghat	80-480	16-3-88	PDH	-	+	No
4 14°02'N-74°45'E	Unchalli Falls	180-220	20-3-87	PDH	-	-	No
5 14°22'N-74°38'E	Doddamane Ghat	50-180	17-3-87	PDH	-	-	No
6 15°23'N-74°21'E	Castle Rock	550-570	21-1-88	MSA	+	-	No
7 15°30'N-74°18'E	Meda	580-620	24-1-88	MSA	+	-	No
8 14°55'N-74°21'E	Anshi Ghat	350-360	9-2-88	PDH	-	-	Seasonal
9 15°N-74°24'E	Anshi (Vakkihalla)	380-440	10-2-88	PDH	-	-	No
10 15°N-74°18'E	Anshi (Bharadi)	510-580	11-2-88	MSA	-	-	No
11 15°N-74°22'E	Talapa (Nujji)	570-580	23-2-88	MSA	-	-	No
12 14°22'N-74°37'E	Methini Ghat	400-410	1-4-86	PDH	+	-	Perennial
13 14°24'N-74°38'E	Aghanashini	30-80	20-3-86	PDH	+	+	No
14 14°15'N-74°45'E	Malemane Ghat	520-560	3-5-86	PDH	+	-	No
15 14°44'N-74°24'E	Makigadde	~40	21-3-88	PDH	+	+	No
16 14°49'N-74°45'E	Manchikere	480-530	18-3-88	MSA	-	-	No
17 14°22'N-74°38'E	Huladevagodlu (Bridge)	110-180	13-3-87	PDH	-	-	No
18 14°23'N-74°38'E	Huladevagodlu	50-160	27-2-87	PDH	-	-	No
19 15°17'N-74°30'E	Jagalbet	610-660	5-1-88	MSA	-	-	Seasonal
20 15°25'N-74°16'E	IB Customs (Karambal) Kaskowadar	~620	23-1-88	MSA	-	-	Seasonal
High disturbance							
1 14°24'N-74°37'E	Badal	80-220	31-3-87	PDH	-	+	No
2 14°24'N-74°36'E	Basalli (Santeguli)	60-100	26-3-87	PDH	-	-	No
3 14°31'N-74°24'E	Nagur Cross	~30	24-4-87	PDH	+	-	Perennial
4 14°30'N-74°30'E	Anegundi-Belangi	~20	5-5-87	PDH	+	+	Seasonal
5 14°31'N-74°30'E	Sandoli	~20	7-5-87	PDH	+	+	Perennial
6 14°39'N-74°50'E	Targod	540-570	20-5-87	PDH	+	-	No
7 15°11'N-74°31'E	Patoli	520-500	4-2-88	MSA	+	-	No
8 14°34'N-74°56'E	Bidralli	~520	18-2-88	PDH	+	-	Seasonal
9 15°22'N-74°30'E	Jagalbet (Bori)	590-600	6-1-88	MSA	-	-	Seasonal
10 15°11'N-74°30'E	Joida	540-560	8-1-88	MSA	-	-	No

\* MSA, '*Memecylon-Syzigium-Actinodaphne*' series of tropical wet evergreen forest. PDH, '*Persea-Diospyros-Holigarna*' series of tropical wet evergreen forest.

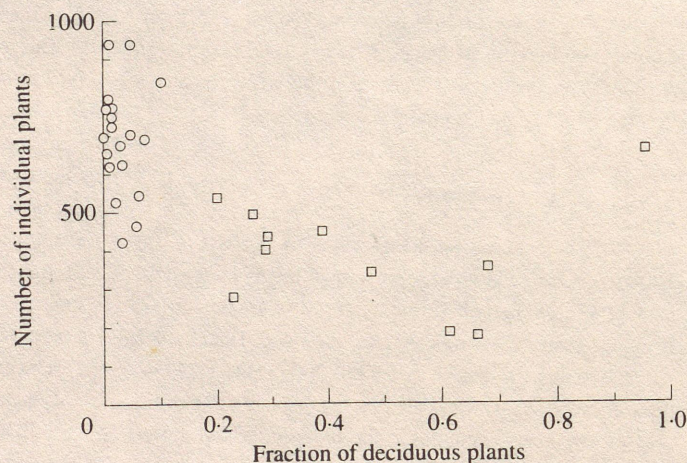


Fig. 2. Distribution of low (O) and high disturbance (□) transects according to the fraction of individuals of deciduous species (x-axis) and the total number of individual plants (y-axis) in each transect.

of numbers of individuals per species, recorded in the different sample plots, does not readily conform to standard distributions; nor are the numbers of plots or individuals

belonging to the two categories equal. We therefore resorted to Monte Carlo simulations to test the null hypothesis that all species were distributed amongst the two

categories without any bias. We performed three kinds of simulations.

1 Distributing the 30 sample sites at random amongst two groups of 20 and 10 each.

2 Distributing the 30 sample sites at random amongst two groups such that each group harboured a number of individual plants as close as possible to that which belonged to each of these two categories, namely 13 886 individuals for low and 3790 for high levels of disturbance.

3 Assigning the individuals belonging to 200 species to the two categories of low and high disturbance with a probability of 13 886/17 676 and 3790/17 676, respectively.

The simulations provide a distribution for the number of species exclusive to the two categories, as well as for the number of shared species, under the null model. These could be compared with the observed values for a statistical validation of our categorization.

### Results and discussion

Table 2 compares the results of the simulations on the basis of these three different assumptions with the actual observations on the number of species exclusive to and number of species shared between the two categories of high and low disturbance. Evidently sites belonging to the two categories harboured a significantly distinctive set of species. As Table 3 shows, the sites belonging to the categories also differed significantly from the expected direction in

**Table 2.** Observed number exclusive to, as well as shared between, sites of low and high disturbance. The expected numbers were obtained, under the null hypothesis of no difference between the two groups, from 1000 Monte Carlo simulations using the models: (1) dividing the populations of 30 sites as observed randomly amongst two groups of 20 and 10; (2) assigning populations at different sites at random amongst two groups such that the total numbers in the two groups were as close as possible to 13 886 and 3790; (3) assigning individual plants randomly to two groups of sites with 13 886 and 3790 individuals, respectively. The probability  $P$  is that of obtaining a value as high as the observed for the number of exclusive species, and as low as the observed for the number of shared species

	Observed	Expected			
			1	2	3
Exclusive to sites of low disturbance	84	$\mu$	54.2	75.5	41.5
		$\sigma$	7.8	9.7	4.0
		Max	79.0	103.0	57.0
		Min	32.0	49.0	30.0
		$P$	<0.001	0.219	<0.001
Exclusive to sites of high disturbance	28	$\mu$	20.7	12.4	5.6
		$\sigma$	5.9	4.7	2.1
		Max	38.0	27.0	13.0
		Min	4.0	1.0	0.0
		$P$	0.099	<0.001	<0.001
Shared between the two sites	88	$\mu$	125.2	112.1	152.8
		$\sigma$	4.5	7.1	3.4
		Max	137.0	131.0	163.0
		Min	109.0	83.0	141.0
		$P$	<0.001	0.003	<0.001

**Table 3.** Number of transects where different agents of disturbance were present

Agent of disturbance	Low disturbance (20 transects)	High disturbance (10 transects)
Grazing	5 (25%)	5 (50%)
Fire	3 (15%)	3 (30%)
Trails	7 (35%)	6 (60%)

The differences in percentages were significant ( $P < 0.05$ ) in all cases.

three measures of disturbance, namely occurrence of trails, pressure of grazing and incidence of fire. None of these differences was initially used to delineate the two categories, and this suggests that we were justified in the conclusion that our 30 sample sites could be divided into two groups of high and low levels of human-induced differences that have favoured the occurrence of distinctive sets of species.

### SPECIES RICHNESS

It was thus appropriate for us to look for differences between these two sets of sites in variables other than the plant density and fraction of deciduous species that were used in deriving the groupings. Species richness, or  $\alpha$ -diversity, and species turnover, or  $\beta$ -diversity, were two such parameters of interest.

One expects two kinds of processes to affect the number of species found on a transect in relation to disturbance. A reduction in plant density would be accompanied by a reduction in the total number of species per unit area, simply because of the decrease in the total number of individuals being sampled. At the same time, opening up of the canopy may lead to a reduction in resource competition, permitting invasion by a large number of species. Indeed, it has been documented that under certain conditions intermediate levels of disturbance lead to an increase in  $\alpha$ -diversity (Connell 1978; Pickett & White 1985; Fuentes & Jaksie 1988).

The 20 evergreen transects harboured between 35 and 62 species, with a mean of 48.8 and a standard deviation (SD) of 5.6. The numbers were lower at the 10 disturbed sites, with a range of 18–55, a mean of 35.7 and with a standard deviation of 11.9. This difference is statistically significant at  $P = 1\%$  ( $t$ -test, Mann-Whitney  $U$ -test). A total of 172 OTUs made up the 13 886 individuals on the 20 evergreen transects; in contrast, only 116 OTUs occurred amongst the 3790 individuals on the 10 disturbed transects. Simulations of sampling 3790 individuals from the total pool of 13 886 individuals of 172 species for the low-disturbance sites provide an estimated mean number of 111 OTUs, with a standard deviation of 6.5. This is slightly lower, but not significantly so, than the 116 species/OTUs amongst the many individuals on the highly disturbed sites. This suggests that the lower number of species on the highly disturbed transects may simply be a consequence of a decrease in density, and may thus be unrelated to any

changes in the packing of species within the community. Values of the exponential of the Shannon-Weaver index  $H = -\sum P_i \ln P_i$ , where  $P_i$  is the fraction of the  $i^{\text{th}}$  species) were also not significantly different for the low as opposed to highly disturbed sites, being  $18.4 \pm 6.1$  for the former and  $15.2 \pm 7.8$  for the latter. In the case of these 10 sites then, an increased level of disturbance was not accompanied by significantly increased levels of  $\alpha$ -diversity.

#### SPECIES TURNOVER

A variety of human disturbances has created a vegetation mosaic in Uttara Kannada. It is possible that in such a landscape a wide range of species may have opportunistically colonized the disturbed patches, with the identity of colonizers differing greatly from patch to patch. This could imply a greater level of species turnover, or  $\beta$ -diversity, for the disturbed patches, even though individual disturbed patches had a lower level of  $\alpha$ -diversity.

By defining  $\beta$ -diversity as the fraction of unshared species between any pair of patches, the highly disturbed sites showed a value of  $0.73 \pm 0.07$  (mean  $\pm$  SD), as opposed to a value of  $0.65 \pm 0.1$  for the low disturbance sites. This difference is significant at the  $P = 1\%$  ( $t$ -test, Mann-Whitney  $U$ -test). However, since the highly disturbed sites had fewer individuals, randomly constituting any pair of such sites from a common pool is expected to give a greater fraction of unshared species. Correcting for this effect, the fraction of unshared species in low disturbance sites is expected to be  $0.70 \pm 0.09$ , which is not significantly different from that of disturbed sites. Thus disturbance did not enhance this component of diversity either.

#### SPECIES ATTRIBUTES

Of the 165 securely identified taxa, 138 occurred on low disturbance sites with 60 being exclusive to them, while 105 occurred on high disturbance sites with 27 being restricted to them. Seventy-eight taxa were shared by high and low disturbance sites. By definition, low disturbance sites had a higher fraction of evergreen species. Species characterized by Pascal (1988) as climax species similarly comprised a higher fraction of the flora on low disturbance sites, while those characterized as pioneers as well as heliophile formed a significantly greater fraction of those restricted to highly disturbed sites (Table 4). Pascal (1988) terms as relicts those evergreen species which persist under disturbance; our data support this contention. No relict species were exclusive to low disturbance sites, but a much greater fraction occurred amongst species shared between low and high disturbance sites than among species restricted to highly disturbed sites alone.

In addition, it is of interest to investigate whether human harvesting more directly favours species with attributes that either (i) hinder harvesting, as with thorns, spines or poisonous latex, or (ii) enhance the species' ability to withstand harvesting, for instance by coppicing. As expected, thorny or latex-bearing plants as well as plants able to be coppiced (Table 4) were significantly

**Table 4.** Number of species with various attributes occurring in low disturbance (L) and high disturbance (H) sites

Attribute	Sites					
	All	L	H	Only L	Only H	L and H
Climax	48	48	0	48	0	0
Deciduous	33	23	31	2	10	21
Evergreen	121	107	65	56	14	51
Coppicing possible	136	110	95	41	26	69
Human demand	54	44	35	19	10	25
Heliophilic	23	16	17	6	7	10
Pioneer	29	22	28	1	7	21
Relict	48	43	48	0	5	43
Thorny	16	11	13	3	5	8
Used for plywood	36	30	23	13	6	17
Used for plywood and possibly coppicing	27	21	21	6	6	15
Used for plywood but not coppicing	9	9	2	7	0	2
Coppicing possible, but no plywood use	109	89	74	35	20	54
Total	165	138	105	60	27	78

less frequent amongst species restricted to low disturbance sites ( $\chi^2$  test,  $P < 0.05$ ).

Finally, plant species differed greatly in the variety of uses to which they were put. These included local subsistence uses such as fuel, small timber or leaf manure, and commercial uses as in the matchwood and plywood industries. The forests of Uttara Kannada have been under the pressure of subsistence use for centuries; in the last 50 years they have come under the pressure of considerable commercial use as well. We therefore scored the species in terms of subsistence use and use in the matchwood and plywood industry. Low and high disturbance sites did not differ significantly in terms of the fraction of species of subsistence or commercial use. However, there was a significant trend when use in the matchwood/plywood industry and coppicing potential were considered in conjunction. Low disturbance sites supported a significantly larger fraction of species ( $\chi^2$  test,  $P < 0.05$ ) demanded by the plywood industry but incapable of being coppiced (Table 4). In other words such species were particularly liable to disappear under high levels of disturbance.

#### BIOMASS DEPLETION

By definition, sites with high levels of disturbance had lower plant densities. But it is of interest to provide a quantitative assessment of the extent of the lowering of biomass levels. The data to hand are restricted to the number of plants of different taxa in each of the seven height classes. This is inadequate for an estimation of absolute levels of biomass, but could be used for an estimation of relative change. Table 5 provides an estimate of the number of plants per 2400 m<sup>2</sup> in each of the seven height classes. While the two sets of sites bore significantly different total numbers of individual plants, there was no significant

**Table 5.** Number of individuals in each of the seven height classes in transects of 2400 m<sup>2</sup>. The numbers are means of 20 transects for the low and of 10 transects for the high disturbance sites

Height class (m)	Disturbance		<i>t</i> -test	<i>U</i> -test
	Low	High		
0-1	149	129	*	NS
1-2	138	70	NS	*
2-4	168	59	**	NS
4-8	93	45	NS	NS
8-16	103	61	NS	**
16-32	41	21	NS	NS
Above 32	2	0.2	NS	NS

\* Significant at 5%.

\*\* Significant at 1%.

NS, not significant ( $P > 0.05$ ).

change in the fraction of plants in the various size classes. This reflects the fact that there have been manifold demands on these forests: while industry requires the larger trees, farmers take out the small trees for fencing poles. If all the plants are taken into account, the density is reduced from 2893 per hectare in sites of low to 1579 in sites of high disturbance, a decline of 45%. The decline is more marked in the height categories of 2-4 m, favoured as poles by villagers, and over 8 m, favoured as timber by commercial interests.

#### BIODIVERSITY LOSSES

There have been a few estimates of biodiversity losses on the Western Ghats (Nair & Daniel 1986). Specifically for Uttara Kannada, five bird species characteristic of forest tracts, namely, *Zoothera dauma*, *Psittacula eupatoria*, *Picus myrmecophonens*, *Treron bicincta* and *Aethopyga siparaja* have apparently disappeared over the last century (Daniels, Joshi & Gadgil 1990). There is also evidence of one plant species having similarly disappeared from this region: a grass *Hubbardia heptaneuron* Bor, recorded only from the spray zone of the Sharavathy river's Jog falls just across the border of Uttara Kannada, has apparently become extinct following the impoundment of the river upstream of the waterfalls. Our data further show that as many as 84 out of 172 OTUs occurring in the low disturbance transects have disappeared locally under high levels of disturbance. This suggests that a number of species characteristic of evergreen forests may be in danger of gradual elimination with increasing disturbance. Notable amongst these are 10 taxa that occurred in seven or more of the 20 low disturbance transects (see Appendix), but were absent from all 10 of the highly disturbed transects. These included two species characteristic of interior evergreen forests, namely *Syzygium gardneri* and *Myristica malabarica*. Both have been exploited by the plywood industry but not by villagers. *M. malabarica* is particularly valued for its fruit, which is collected and marketed by villagers who do not cut the tree. *Holigarna grahamii* is also exploited by the

industry, but is left untouched by the local people because of its poisonous latex. Three other evergreen species characteristic of low disturbance transects but absent from highly disturbed ones have been used both by industry and by the villagers as small timber. These are *Calophyllum polyanthum*, *Dysoxylon malabaricum* and *Polyalthia fragrans*. The woody gymnospermous climber *Gnetum ula* and many species of the angiospermous vine genus *Piper* similarly characterized low-disturbance tracts, but have disappeared from all highly disturbed transects. These climbers have been subject to regular 'climber-cutting' as part of silvicultural practices prescribed by the Forest Department. Three other widespread evergreen species that disappear under disturbance, *Dichapetalum gelanioides*, *Elaeocarpus* sp. and *Neolitsea zeylanica* have not been in industrial demand and seem to have been affected primarily by village-level utilization and changes in the microclimate that accompanies opening of the canopy.

A much smaller number of species absent from low-disturbance sites, namely 28, colonized highly disturbed tracts. Notable amongst these were seven species that were common under high levels of disturbance, occurring in four out of 10 transects. These included *Albizia odoratissima*, *Cassia fistula*, *Dalbergia latifolia* (rosewood), *Lannea coromandelica*, *Schleichera oleosa*, *Tectona grandis* (teak) and *Xeromphis uliginosa*. Two of these, rosewood and teak, have been highly valued as timber species. All these seven species have a widespread distribution over the Indian subcontinent and in south-east Asia, and are thus of much lower conservation value compared with the evergreen species with more restricted geographical ranges. It would therefore appear that the high levels of disturbance which are now endemic over much of the Western Ghats may be responsible for considerable levels of biomass loss, as well as for local extinctions of several evergreen tree species of high conservation value.

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## Appendix

A list of species found in at least four of the transects is shown below together with their attributes\*. The columns headed L and H indicate the number of transects in the localities with low and high levels of disturbance where the species was present; IL and IH denote the total number of individuals of the species recorded in low- and high-disturbance localities.

Species name	Attributes*	L	H	IL	IH
Exclusive to low disturbance sites					
1 <i>Arenga wightii</i> Griff.	C . E . . . . .	6	0	239	0
2 <i>Calophyllum polyanthum</i> Wall ex Choisey	C . E . G . . . . . W	12	0	142	0
3 <i>Carallia brachiata</i> (Lour.)	. . . E F . H . . . . . W	5	0	8	0
4 <i>Dichapetalum gelanioides</i> (Roxb.) Engl.	C . E F . . . . .	13	0	743	0
5 <i>Dysoxylon malabaricum</i> Bedd.	C . E F G . . . . . W	13	0	342	0
6 <i>Dracaena terniflora</i> Roxb.	C . E F . . . . .	5	0	23	0
7 <i>Elaeocarpus</i> sp.	C . E F . . . . . W	13	0	264	0
8 <i>Ficus nervosa</i> Heyne ex Roth	C . E F G . . . . . W	6	0	7	0
9 <i>Gnetum ula</i> Brong.	. . . E F . . . . . L . . . . .	9	0	42	0
10 <i>Holigarna grahamii</i> (Wight) Kurz	C . E F G . . . . . W	12	0	169	0
11 <i>Liitsea</i> sp.	C . E F . . . . .	4	0	16	0
12 <i>Mammea suriga</i> (Buch. Ham ex Roxb.) Kost	C . E F . . . . .	4	0	7	0
13 <i>Murraya paniculata</i> (L.) Jack.	C . E F . . . . .	4	0	12	0
14 <i>Myristica dactyloides</i> Gaertn.	C . E . . . . . W	5	0	21	0
15 <i>Myristica malabarica</i> Lam.	C . E . . . . . W	15	0	278	0
16 <i>Neolitsea zeylanica</i> (Nees) Merr.	C . E F . . . . .	8	0	84	0
17 <i>Ochlandra</i> sp.	C . E F G . . . . .	4	0	155	0
18 <i>Piper</i> spp.	C . E F . . . . .	13	0	559	0
19 <i>Polyalthia fragrans</i> (Dalz.) Bedd.	C . E F G . . . . . W	7	0	128	0

\* The attribute codes are: C, climax; E, evergreen; G, human demand (non-plywood); I, introduced (plantations, etc.); P, pioneer; T, thorny/toxic; D, deciduous; F, able to be coppiced; H, heliophilic; L, liana; R, relict; W, used by the plywood industry.

## Appendix Continued

Species name	Attributes*	L	H	IL	IH
20 <i>Reinwardtiendron</i> <i>animalaiense</i> (Bedd.) Mabb.	C.E.....	4	0	96	0
21 <i>Strombosia ceylanica</i> Gardn.	C.EFG.....	8	0	159	0
22 <i>Symplocos racemosa</i> Roxb.	C.E.....	4	0	44	0
23 <i>Syzigium gardneri</i> Thwaites	C.E.G.....W	12	0	298	0
Common to both high- and low-disturbance sites					
1 <i>Actinodaphne malabarica</i> Balakr.	..EF.....R..	15	3	69	8
2 <i>Alstonia scholaris</i> (L.) R.Br.	..EFG.....R.W	1	5	1	6
3 <i>Alseodaphne semecarpifolia</i> Nees	..EFG.....R.W	1	5	6	19
4 <i>Ancistrocladus heyneanus</i> Wall ex Grab.	...F...L.R..	10	1	130	1
5 Annonaceae -I	..E.....R..	5	3	8	12
6 <i>Aporosa lindleyana</i> Blume.	..EFGH.....	11	5	139	258
7 <i>Artocarpus hirsutus</i> Lam.	..EFG.....R.W	5	1	7	1
8 <i>Bauhinia racemosa</i> Lam.	..D.F....P..W	1	3	1	4
9 <i>Buchanania lanzen</i> Sprengel	..D.FG....P...	1	3	1	5
10 <i>Calycopteris floribunda</i> Lam.	...F...L.R..	6	10	13	160
11 <i>Callicarpa tomentosa</i> (L.) Murr.	..EF.H.....	10	6	38	12
12 <i>Calamus</i> sp.	...F.....RT.	15	1	1013	1
13 <i>Careya arborea</i> Roxb.	..D.F....P...	7	9	17	78
14 <i>Caryota urens</i> L.	..E.....R..	9	2	21	2
15 <i>Cinnamomum</i> sp.	..EFG.....R.W	19	3	289	5
16 <i>Dillenia pentagyna</i> Roxb.	..D.F....P..W	5	8	8	36
17 <i>Dimocarpus longan</i> Lour.	..EF.....R..	12	1	186	7
18 <i>Diospyros buxifolia</i> (Blume) Hiern	..EFG.....R.W	3	1	92	18
19 <i>Diospyros</i> sp.	..EF.....R..	20	3	546	13
20 <i>Emblica officinalis</i> Gaertn.	..D.F....P...	2	6	2	54
21 <i>Ervatamia heyneana</i> (Wall) Cooke	..D.F....P...	9	8	31	138
22 <i>Syzigium</i> sp.	..E.G....R.W	18	1	169	1
23 <i>Syzigium cumini</i> (L.) Skeels	..EF.....R.W	2	3	5	11
24 Euphorbiaceae-I	..E.....R..	5	1	36	3
25 <i>Ficus</i> sp.-I	..EF.....R..	2	2	9	2
26 <i>Ficus</i> sp.-II	..EF.....R..	5	4	7	5
27 <i>Flacourtia montana</i> Grah.	...F.....RT.	8	2	50	46
28 <i>Garcinia indica</i> (Dup.-Thou) Choisy	..E.G....R..	4	1	5	2
29 <i>Garcinia</i> sp.	..EFG.....R..	13	2	159	3
30 <i>Gmelina arborea</i> Roxb.	..D.FG....P..W	2	4	12	14
31 <i>Grewia tiliifolia</i> Vahl.	..D.FG....P...	6	5	9	56
32 <i>Holigarna arnottiana</i> Hook.f.	..EF.....R.W	8	2	36	2
33 <i>Hopea ponga</i> (Dennst.) Mabb.	..EFG.....R..	12	4	658	39
34 <i>Hydnocarpus pentandra</i> (Buch-Ham.) Oken	..EF.....R..	4	2	8	4
35 <i>Ixora brachiata</i> Roxb.	..EFG.....R..	12	4	147	69
36 <i>Ixora</i> sp.	..EF.....R..	3	2	51	23
37 <i>Knema attenuata</i> (Hook.f. & Thomson) Warb	..EF.....R.W	16	1	670	19
38 <i>Lagerstroemia microcarpa</i> Wight	..D.FG....P..W	8	8	35	77
39 <i>Leea indica</i> (Burm.f) Merr.	..EF.....R..	20	6	473	118
40 <i>Macaranga peltata</i> (Roxb.) Muell. Arg.	..EF.H.....	13	9	134	53
41 <i>Mallotus philippensis</i> (Lam.) Muell. Arg.	..EF.H.....	7	4	36	17
42 <i>Mangifera indica</i> L.	..EFG.....R.W	13	2	27	2
43 <i>Maytenus rothiana</i> (Walp.) Raman	..EF.....R..	10	3	97	9
44 <i>Melia dubia</i> Cav.	..EFGH.....	3	1	3	1
45 <i>Memecylon</i> sp.	..EFG.....R..	10	2	1339	21
46 <i>Mimusops elengi</i> L.	..EF.....R.W	3	1	3	2
47 <i>Moullava spicata</i> (Dalz.) Nicols	..EF.....T..	4	4	14	12
48 <i>Murraya koenigi</i> (L.) Sprengel	..E..H.....	2	3	28	146
49 <i>Nothopodytes nimmoniana</i> (Grah.) Mabb.	..EF.....R..	15	3	108	9
50 <i>Nothopegia</i> sp.	..EF.....R..	14	1	163	4

\* The attribute codes are: C, climax; E, evergreen; G, human demand (non-plywood); I, introduced (plantations, etc.); P, pioneer; T, thorny/toxic; D, deciduous; F, able to be coppiced; H, heliophilic; L, liana; R, relict; W, used by the plywood industry.

## Appendix Continued

Species name	Attributes*	L	H	IL	IH
51 <i>Olea dioica</i> Roxb.	. . . EFGH . . . . .	19	3	369	32
52 <i>Oxytenanthera</i> sp.	. . . EFGH . . . . .	2	6	14	693
53 <i>Persea macrantha</i> (Nees) Kosterm.	. . . EFG . . . . R . W	10	1	78	7
54 <i>Psychotria dalzellii</i> Hook. f.	. . . EF . . . . . R . .	15	4	321	8
55 <i>Pterospermum</i> sp.	. . D . F . . . . . P . . .	11	3	133	25
56 <i>Xeromphis spinosa</i> (Thunb.) Keay	. . . EF . . . . . T .	9	6	46	41
57 Rutaceae -I	. . . EF . . . . . R . .	10	4	119	143
58 Sapindaceae -I	. . . EF . . . . . R . .	2	3	110	15
59 <i>Sterculia guttata</i> Roxb. ex DC.	. . . D . F . . . . . P . . .	3	2	9	8
60 <i>Stereospermum personatum</i> (Hask.) Chatt.	. . . D . F . . . . . P . . W	3	5	3	13
61 <i>Strychnos nux-vomica</i> L.	. . . EF . . . . . TW	1	5	1	19
62 <i>Terminalia bellarica</i> (Gaertn.) Roxb.	. . . D . FG . . . . P . . W	6	4	12	5
63 <i>Terminalia paniculata</i> (Roxb.) Rath	. . . D . FG . . . . P . . W	13	10	72	262
64 <i>Terminalia alata</i> Heyne ex Roth.	. . . D . FG . . . . P . . W	4	4	22	31
65 <i>Vitex altissima</i> L.f.	. . . D . F . . . . . P . . .	6	3	17	4
66 <i>Xantolis tomentosa</i> (Roxb.) Raf.	. . . EF . . . . . T .	1	3	2	5
67 <i>Xylia xylocarpa</i> (Roxb.) Taub.	. . . D . F . . . . . P . . .	1	9	29	210
68 <i>Zyziphus</i> sp.	. . . . . F . H . . . . . T .	2	8	2	28
Exclusive to highly disturbed sites					
1 <i>Albizia odoratissima</i> (L.f.) Benth.	. . . D . F . . . . . P . . .	0	4	0	6
2 <i>Cassia fistula</i> L.	. . . D . FG . . . . P . . .	0	5	0	8
3 <i>Dalbergia latifolia</i> Roxb.	. . . D . FG . . . . P . . W	0	5	0	7
4 <i>Lannea coromandelica</i> (Houtt.) Merr.	. . . D . FG . . . . . W	0	5	0	9
5 <i>Schleichera oleosa</i> (Lour.) Oken	. . . D . FG . . . . P . . .	0	6	0	64
6 <i>Tectona grandis</i> L.f.	. . . . . F . . . I . . . . W	0	5	0	69
7 <i>Xeromphis uliginosa</i> (Retz.) Maheshwary, J.	. . . EF . . . . . T .	0	4	0	20

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