

Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India

R. Sukumar, H. S. Dattaraja, H. S. Suresh, J. Radhakrishnan, R. Vasudeva, S. Nirmala and N. V. Joshi

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

As part of an international network of large plots to study tropical vegetation dynamics on a long-term basis, a 50-hectare permanent plot was set up during 1988–89 in the deciduous forests of Mudumalai, southern India. Within this plot 25,929 living woody plants (71 species) above 1 cm DBH (diameter at breast height) were identified, measured, tagged and mapped. Species abundances corresponded to the characteristic log-normal distribution. The four most abundant species (*Kydia calycina*, *Lagerstroemia microcarpa*, *Terminalia crenulata* and *Helicteres isora*) constituted nearly 56% of total stems, while seven species were represented by only one individual each in the plot. Variance/mean ratios of density showed most species to have clumped distributions. The population declined overall by 14% during the first two years, largely due to elephant and fire-mediated damage to *Kydia calycina* and *Helicteres isora*. In this article we discuss the need for large plots to study vegetation dynamics.

RESEARCH ON forests has been going on for several decades and yet we do not precisely understand their ecology. This is especially true of tropical forest ecology. It is well known that tropical forests are amongst the richest biological communities on earth. The disappearance of these forests, at an estimated rate of 1–2% per year¹, comes at a time when our knowledge of their structure and dynamics is woefully inadequate².

With a few exceptions, ecological studies of tropical forests have been largely isolated efforts, on small spatial scales and over short time periods. Notable

among the exceptions are the ongoing research on Barro Colorado Island in Panama by the Smithsonian Tropical Research Institute^{3,4} and the La Selva Biological Reserve in Costa Rica by the Organization for Tropical Studies⁵, both in the Neotropics.

Unlike in the relatively species-poor temperate forests, the study and characterization of species-rich tropical forests is a far more complex task. For one, the distribution of plant species is very heterogeneous, with most species having clumped distributions, making it necessary to study a large area in order to get an unbiased representation of the species present in the study sample. There is also a very wide variation in the relative abundance of species; a large study plot is again needed to provide sufficiently large sample sizes for the less common plants if one is to do any meaningful statistical analyses. Year to year variations in life-history phenomena of individuals and populations in response to climatic fluctuations (hurricanes, for instance, cause tremendous changes) also make long-term studies important.

Studies of tropical forests had been mostly confined to sampling trees within one or a few hectares until Hubbell and Foster^{6,7} took a bold step by setting up a 50-ha permanent plot in the tropical evergreen forests of Barro Colorado Island during 1980–82. Not only trees but also all other woody plants, excluding lianas, down to 1 cm stem DBH (diameter at breast height, in this case 1.3 m height) were enumerated and mapped. This provided an unprecedented opportunity to follow in detail the life histories of species, their interactions and the dynamics of plant communities.

This was soon followed during 1985–88 by another similar-sized plot in the equatorial rain forests of Pasoh Reserve in Peninsular Malaysia, set up by the Malaysian Forest Research Institute⁸, in collaboration with Peter Ashton of the Harvard University and Stephen Hubbell of the Princeton University.

These two 50-ha vegetation plots involved considerable effort in the field. In the Panamanian plot about 238,000 individuals from 302 species were enumerated, while in the Malaysian plot there were 340,000 individuals from 818 species.

The Indian Institute of Science has been involved since 1980 in the setting up of the Nilgiri Biosphere Reserve in southern India and had a commitment towards long-term ecological research that would contribute to the management of the reserve. Fundamental to the research programme is an understanding of the dynamics of the diverse forest types that are found here. The vegetation ranges from dry thorn forest in the low rainfall (500 mm annually) eastern regions through deciduous forest to montane stunted evergreen forest on the summit of the Nilgiri plateau to wet evergreen forests along the western slopes which enjoy copious rainfall (over 5000 mm annually) (refs. 9,10). The plant species diversity varies tremendously across these vegetation types from about 9–13 species above 10 cm DBH within 0.1 ha in the deciduous forests to 34–49 species in the montane *shola* forests and 36–41 species in the lower elevation wet evergreen forests^{9,11,12}.

When we began our research programme here, we had to make choices regarding the locations of our study sites amongst this vegetational diversity and the design of the study plots. We decided to join the international network of 50-ha plots that were being promoted by Hubbell. Considering the logistical problems in setting up such a large plot, this meant that only a single plot was possible, at least in the beginning.

We also selected the relatively species-poor deciduous forests of Mudumalai Sanctuary for our study for a number of reasons. Firstly, this would ideally complement the Panamanian (tropical semi-evergreen forest) and the Malaysian (equatorial evergreen forest) sites by its being a different vegetation type. Factors influencing the vegetation dynamics of a deciduous forest can be expected to be rather different from those driving the dynamics of rain forests. In rain forests, for instance, the size, shape, orientation and seasonal timing of canopy gaps influence the regeneration and subsequent establishment of woody species, particularly heliophilic pioneers (refs. 7, 13–15; also see the papers in *Ecology*, June 1989). On the other hand, gaps may be relatively less important in influencing the dynamics of a relatively open-canopied forest almost resembling a savanna woodland in its physiognomy. Other factors such as fire and large mammals can be expected to play major roles in the dynamics. Fire is an almost annual occurrence in

these forests and causes high mortality of saplings. Large mammals such as elephants alter the vegetation significantly by damaging or pushing over trees. The three sites in different vegetation types with their own peculiar environmental conditions would thus permit a comparative approach to the study of forest dynamics. A second reason for selecting the deciduous forest was that this had been traditionally a source of timber, and thus our study of these logged forests could potentially generate the scientific information for future sustainable management of similar forests for timber and other products. A third reason for selecting the deciduous forest was that this would complement our own ongoing research here on the large mammal populations, thus providing a more comprehensive picture of ecosystem dynamics.

In this article we merely describe the basic field methods adopted by us, present the preliminary results of the study based on static data from the first enumeration and discuss the issue of whether we were justified in setting up a single large plot of 50 ha.

The study area

Mudumalai Sanctuary extending over 321 km² is situated to the north of the Nilgiri plateau (11°32' to 11°43' N, 76°22' to 76°45' E) at an altitude of 850–1250 m above MSL in the Tamil Nadu state of southern India (Figure 1). A distinct rainfall gradient extends from west (higher rainfall, average 1800 mm per annum) to east (lower rainfall, average 800 mm per annum), with a corresponding change in vegetation type from moist deciduous forest (*Lagerstroemia-Tectona-Terminalia* series) through dry deciduous forest

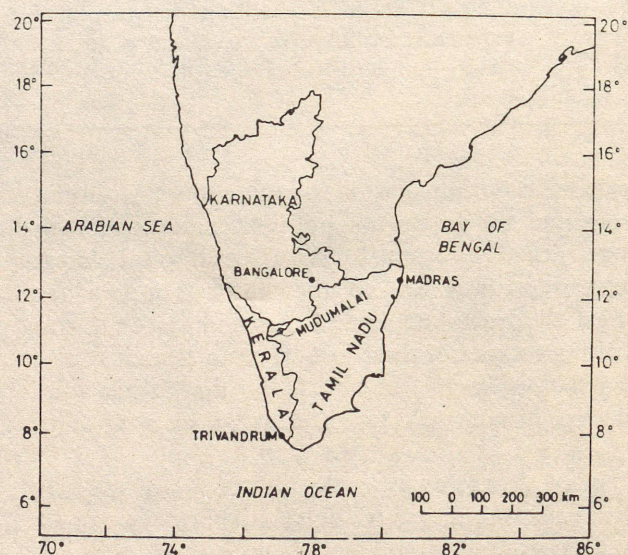


Figure 1. Map showing the location of Mudumalai Sanctuary in the Tamil Nadu state of southern India.

(*Anogeissus-Tectona-Terminalia* series) to dry thorn forest (*Acacia-Ziziphus* series) (for more details of vegetation types and floristics see Sharma *et al.*¹¹, Puri *et al.*¹⁶, Bellan¹⁷). The moister regions in the west have swampy grasslands (or *vyals*) extending through the forest. *Bambusa arundinacea* is common in the moister forests and along stream banks in the drier tract. The understorey is dominated by perennial grasses, particularly of the genus *Themeda* (*T. cymbaria* and *T. triandra*). In the more disturbed areas the undergrowth also features the weeds *Chromolaena odorata*, *Lantana camara* and *Spatholobus parviflorus*.

Aims of the study

We had the following broad questions in mind while initiating this study.

The structure of a deciduous forest community

What are the patterns of abundances of different canopy trees, understorey trees and shrubs? How are these species distributed in space? Do they have even, random or clumped distributions? Are there differences between the more common and rarer species in dispersion patterns? How are saplings distributed in relation to their adult conspecifics? Could species distributions be explained by topography such as degree of slope? What are the species-specific positive, neutral or negative associations?

The dynamics of the community

What are the patterns of recruitment, growth and mortality of species? Are the populations of these increasing, stable or decreasing in the plot? How does fire effect the dynamics of the community? What role do large mammals such as elephants play in the dynamics through debarking, breaking stems or even pushing over trees?

How does intra- and inter-specific competition shape the structure of a community? For instance, do saplings perform better if close to a conspecific or a heterospecific? In what direction is succession taking the community; specifically, is the community moving towards an equilibrium or is it constantly in a state of nonequilibrium over the 50-ha spatial scale?

Implications for management

One important goal of the study is to make recommendations for scientific management of such tropical forests based on the results of ecological research. What is the best strategy for harvesting timber

trees in deciduous forests? How can these forests be managed for fire to ensure optimum regeneration?

Basic field methods

After a preliminary reconnaissance of Mudumalai Sanctuary during 1987 we selected a 50-ha block of forest (11°35'41" to 11°35'57" N, 76°31'50" to 76°32'22" E) in Compartment 17 of Kargudi Range in the heart of the sanctuary. One of the important requisites of a site, namely that it should not be subject to any present or anticipated disturbance in future through felling of trees or grazing by domestic livestock, was fulfilled here.

The work began in February 1988 with survey and gridding of the plot using a theodolite. The plot running 1 km west to east and 0.5 km south to north was gridded into quadrats of 20 m × 20 m (projected in space), making appropriate corrections for slope. Due to the very hilly nature of the terrain there were considerable problems in ensuring accurate survey and gridding. Aluminium pipes with the x and y axis coordinates stamped were installed as boundary markers. The enumeration began in May 1988, proceeded concurrently with the gridding, and was completed in May 1989.

For the enumeration each 20 m × 20 m quadrat was temporarily subdivided into four 10 m × 10 m sub-quadrats with ropes. All living woody plants above 1 cm DBH were identified, measured for DBH, numbered with an aluminium tag and their locations mapped to the nearest 10 cm (in practice the accuracy was probably about 0.5 m). Individuals with multiple stems from below or above ground branches were given a single number, though all the stems were separately measured. For plants above 10 cm DBH the number tags were nailed on to the stem, while for smaller plants they were threaded through an aluminium wire which was tied around the stem to prevent any injury. We used aluminium wire which had the capacity to withstand possible melting from the fires that regularly sweep these forests. Damage to plants by mammals, insects or other causes was recorded. Bamboos were also enumerated; they were not measured but the number of culms in each clump was noted. Standing dead trees above 10 cm DBH alone were enumerated to get an idea of mortality patterns. Within each quadrat and hectare the enumeration proceeded in a clockwise direction beginning with the southwest corner, and from one hectare to another in a south to north direction.

We have tried to ensure that disturbance to the plot from enumerators is minimal. The breaking of saplings or introduction of seeds of exotic plants (such as fruits that may be eaten) are not permitted. While doing the theodolite survey it was inevitable that some

of the tall grasses or weeds such as *Chromolaena* were pushed aside when these obstructed the line of sighting. Similarly, some trampling of soil in the plot was inevitable. These were not expected to be serious disturbances, because they in any case also occur naturally through the action of the abundant elephant and other large mammal populations here.

Results

Vegetation composition and species abundances

The 50-ha plot contained 25,929 living individual woody plants above 1 cm DBH, coming from 71 species (including one bamboo species) during the first enumeration (Table 1). In addition, 955 standing dead stems above 10 cm DBH of 31 species were recorded. The most common species in the plot was *Kydia calycina*, an understory tree, with 5175 individuals constituting 20% of the total enumerated woody plant population, while the second most abundant was *Lagerstroemia microcarpa*, a canopy tree, with 3980 individuals (15.3%). At the rare end of the scale were seven species with only one individual each in the entire 50 ha, while as many as 45 species had average densities of less than one individual per hectare. The four most common species made up 55.9%, the eight most common species made up 83.2% and the 12 most common species made up 90.6% of all individuals. A very few species thus dominate the community numerically.

The genus with the largest number of species was *Ficus* (Moraceae) with five species in the plot. *Ficus* were however among the most rare, with only 3–12 individuals per species. This was followed by the genus *Terminalia* (Combretaceae) with three species, represented by 34 (*T. bellirica*), 61 (*T. chebula*) and 2776 (*T. crenulata*) individuals. There were seven genera with two species each, while the remaining 50 genera were monospecific in the plot.

The most common family was Fabaceae (13 species), followed by Moraceae (6 species), Rubiaceae and Euphorbiaceae (5 species each).

When the species abundances are represented on a semilogarithmic scale—the abundance on a \log_2 scale and the number of species on an arithmetic scale—the pattern is seen to largely correspond to the familiar log-normal distribution (Figure 2) (ref. 18). Towards the abundant end of the scale there are more than an expected number of co-dominant species with abundances of 2048–4096 individuals each. With *Kydia calycina*, the most common species reducing to below 4000 by the year 1989 itself, thus moving into this octave, the last octave became even more pronounced. This may have some biological significance in that it may be an indicator of a disturbed community.

Patterns of dispersion

Most of the species show clumped pattern of dispersion. The variance to mean ratio of density of a species is a simple yet reasonably robust measure of its dispersion pattern^{19,20}. The variance/mean ratio of 26 species with over 50 individuals in the plot (i.e. at least one individual per hectare on average) is given in Table 2 for three varying plot sizes—0.04 ha, 0.25 ha and 1.0 ha. A ratio of 1.0 indicates a random dispersion, less than 1.0 an uniform dispersion and greater than 1.0 an increasingly clumped dispersion.

The two most abundant species, *Kydia calycina* and *Lagerstroemia microcarpa*, along with *Helicteres isora* (ranked fourth) also show the highest degrees of clumping. On the other hand, no species has a variance/mean ratio below 1.0, indicating that none approaches a uniform dispersion pattern. On a 0.04-ha scale a number of species have ratios from 1.0 to 2.0, which indicates a near-random dispersion. At the larger scale of 1 ha, the ratios increase substantially for practically all species. One exception to this is *Gmelina arborea*, which still maintains a ratio suggestive of a random dispersion even at the larger plot sizes. Among the very abundant species, *Tectona grandis* shows the least clumping. It is not clear at this stage whether this is the natural pattern for this species or an artefact arising from its selective harvest in the past for timber.

Patterns of regeneration

Figure 3 gives the size class frequency distribution of all individuals in the 50-ha plot. Assuming that growth is linear and that mortality rates are monotonic across all size classes and species, it can be seen that there is a deficiency of individuals in the smallest size class. The above assumptions are, however, too simplistic.

Individual species can certainly be expected to show enormous differences in life-history patterns. The size class frequency distributions also show very different patterns in the species. Some species have few or no individuals in the smallest size class (below 5 cm DBH) compared to the larger size classes. These include *Anogeissus latifolia*, *Grewia tiliifolia*, *Eriolaena quinquelocularis*, *Diospyros montana*, *Ougeinia oojeinensis*, *Schleichera oleosa*, *Gmelina arborea*, *Terminalia chebula*, *Bridelia retusa*, *Bombax ceiba* and *Terminalia bellirica*.

The implications of this apparent 'lack of regeneration' for the future dynamics of these species are not clear. It would be fallacious to directly equate size class with age class of a species²¹. What is more relevant for population dynamics is the age distribution of a species in relation to its other demographic traits. Inferences about whether a species is increasing, stable or declining can usually be made after censuses conducted

Table 1. List of all species in order of abundance in the 50-ha plot

Species (Family)	Total no. of individuals	No. of ha of occurrence	Total (%)	Cumulative percentage
<i>Kydia calycina</i> Roxb. (Malvaceae)	5175	49	19.96	19.96
<i>Lagerstroemia microcarpa</i> Wight. (Lythraceae)	3980	49	15.35	35.31
<i>Terminalia crenulata</i> Roth. (Combretaceae)	2776	50	10.71	46.01
<i>Helicteres isora</i> L. (Sterculiaceae)	2571	43	9.91	55.93
<i>Anogeissus latifolia</i> (DC.) Wall.ex Guill. & Perr. (Combretaceae)	2280	50	8.79	64.72
<i>Tectona grandis</i> L. f. (Verbenaceae)	2143	50	8.26	72.99
<i>Cassia fistula</i> L. (Fabaceae)	1881	50	7.25	80.24
<i>Xeromphis spinosa</i> (Thunb.) Keay. (Rubiaceae)	770	46	2.97	83.21
<i>Emblica officinalis</i> Gaertner. (Euphorbiaceae)	577	49	2.22	85.44
<i>Grewia tiliifolia</i> Vahl. (Tiliaceae)	539	50	2.08	87.52
<i>Syzygium cumini</i> (L.) Skeels. (Myrtaceae)	415	46	1.60	89.12
<i>Bambusa arundinacea</i> (Retz.) Roxb. (Poaceae)	381	29	1.47	90.59
<i>Radermachera xylocarpa</i> (Roxb.) Schum. (Bignoniaceae)	357	47	1.38	91.96
<i>Eriolaena quinquelocularis</i> (Wt. & Arn.) Clegh. (Sterculiaceae)	251	46	0.97	92.93
<i>Cordia obliqua</i> Willd. (Boraginaceae)	197	44	0.76	93.69
<i>Diospyros montana</i> Roxb. (Ebenaceae)	130	32	0.50	94.19
<i>Stereospermum colias</i> (Dillw.) Mabberley. (Bignoniaceae)	123	10	0.47	94.67
<i>Ougeinia oojeinensis</i> (Roxb.) Hochr. (Fabaceae)	111	10	0.43	95.09
<i>Lagerstroemia parviflora</i> Roxb. (Lythraceae)	92	18	0.35	95.45
<i>Shorea roxburghii</i> Don. (Dipterocarpaceae)	79	8	0.30	95.75
<i>Cordia wallichii</i> G. Don. (Boraginaceae)	78	27	0.30	96.05
<i>Dalbergia latifolia</i> Roxb. (Fabaceae)	76	22	0.29	96.37
<i>Schleichera oleosa</i> (Lour.) Oken. (Sapindaceae)	75	29	0.29	96.64
<i>Schrebera swietenoides</i> Roxb. (Oleaceae)	69	15	0.27	96.90
<i>Terminalia chebula</i> (Gaertn.) Retz. (Combretaceae)	61	26	0.23	97.14
<i>Gmelina arborea</i> Roxb. (Verbenaceae)	60	32	0.23	97.37
<i>Casearia esculenta</i> Roxb. (Flacourtiaceae)	47	26	0.18	97.55
<i>Bridelia retusa</i> (L.) Spreng. (Euphorbiaceae)	40	20	0.15	97.70
<i>Bombax ceiba</i> L. (Bombacaceae)	38	21	0.15	97.85
<i>Terminalia bellirica</i> (Gaertn.) Roxb. (Combretaceae)	34	23	0.13	97.98
<i>Butea monosperma</i> (Lam.) Taub. (Fabaceae)	34	9	0.13	98.11
<i>Careya arborea</i> Roxb. (Lecythidaceae)	34	21	0.13	98.24
<i>Garuga pinnata</i> Roxb. (Burseraceae)	32	15	0.12	98.37
<i>Ziziphus xylopyrus</i> Willd. (Rhamnaceae)	31	15	0.12	98.49

Table 1. Continued

<i>Cassine glauca</i> (Rottb.) Kuntze. (Celastraceae)	31	4	0.12	98.61
<i>Bauhinia malabarica</i> Roxb. (Fabaceae)	30	21	0.12	98.72
<i>Mallotus philippensis</i> (Lam.) Muell. (Euphorbiaceae)	28	6	0.11	98.83
<i>Indigofera cassioides</i> Rottler ex DC. (Fabaceae)	22	4	0.08	98.92
<i>Pterocarpus marsupium</i> Roxb. (Fabaceae)	22	13	0.08	99.00
<i>Cassia montana</i> Heyne ex Roth. (Fabaceae)	21	4	0.08	99.08
<i>Canthium dicoccum</i> (Gaert.) T. & B. (Rubiaceae)	20	12	0.08	99.16
<i>Mitragyna parvifolia</i> (Roxb.) Korth. (Rubiaceae)	20	12	0.08	99.24
<i>Allophylus cobbe</i> (L.) Raeusch. (Sapindaceae)	19	6	0.07	99.31
<i>Hymenodictyon orixense</i> (Roxb.) Mabberley (Rubiaceae)	14	10	0.05	99.36
<i>Semecarpus anacardium</i> L. f. (Anacardiaceae)	14	12	0.05	99.42
<i>Antidesma diandrum</i> Roth. (Euphorbiaceae)	13	7	0.05	99.47
<i>Ficus virens</i> Aiton. (Moraceae)	12	10	0.05	99.51
<i>Lanea coromandelica</i> (Houtt.) Merr. (Anacardiaceae)	12	9	0.05	99.56
<i>Bauhinia racemosa</i> Lam. (Fabaceae)	11	3	0.04	99.60
<i>Ficus tsjahela</i> Burman. (Moraceae)	11	10	0.04	99.64
<i>Albizia odoratissima</i> (L. f.) Benth. (Fabaceae)	9	6	0.03	99.68
<i>Dalbergia lanceolaria</i> L. f. (Fabaceae)	9	7	0.03	99.71
<i>Flacourtia indica</i> (N. Burm.) Merrill. (Flacourtiaceae)	8	8	0.03	99.74
<i>Wrightia tinctoria</i> R. Br. (Apocyanaceae)	8	7	0.03	99.78
<i>Ziziphus rugosa</i> Lam. (Rhamnaceae)	8	2	0.03	99.81
<i>Olea dioica</i> Roxb. (Oleaceae)	7	5	0.03	99.83
<i>Ficus religiosa</i> L. (Moraceae)	7	6	0.03	99.86
<i>Erythrina indica</i> Lam. (Fabaceae)	6	5	0.02	99.88
<i>Pavetta tomentosa</i> Roxb. ex J.E. SM. (Rubiaceae)	5	1	0.02	99.90
<i>Grewia hirsuta</i> Vahl. (Tiliaceae)	5	3	0.02	99.92
<i>Mangifera indica</i> L. (Anacardiaceae)	4	4	0.01	99.94
<i>Ficus drupacea</i> Thumb. (Roth.) Corne (Moraceae)	4	3	0.01	99.95
<i>Ficus benghalensis</i> L. (Moraceae)	3	3	0.01	99.96
<i>Premna tomentosa</i> Willd. (Verbenaceae)	2	1	0.01	99.97
<i>Artocarpus gomezianus</i> Wall. ex Trecul. (Moraceae)	1	1	0.00	99.98
<i>Chukrasia tabularis</i> A. Juss. (Meliaceae)	1	1	0.00	99.98
<i>Vitex altissima</i> L. f. (Verbenaceae)	1	1	0.00	99.98
<i>Bischofia javanica</i> Blume. (Euphorbiaceae)	1	1	0.00	99.99
<i>Crotalaria</i> sp. (Fabaceae)	1	1	0.00	99.99
<i>Buchanania axillaris</i> (Desr.) Ramam. (Anacardiaceae)	1	1	0.00	99.99
Unidentified	1	1	0.00	100.00

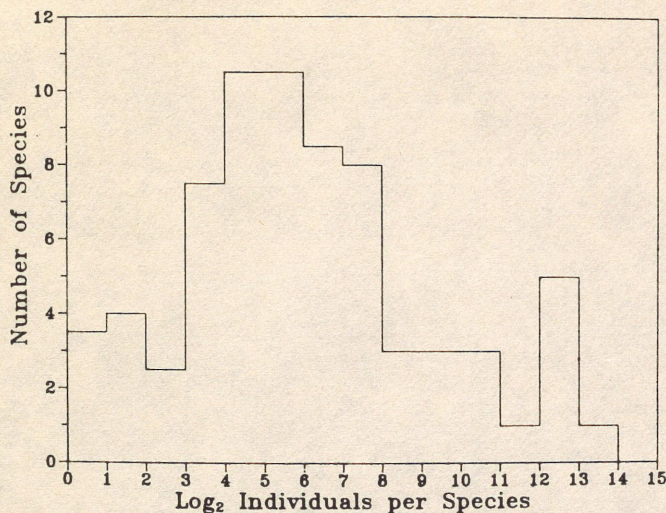


Figure 2. Species abundances for the 71 species in the 50-ha plot. Abundance categories are in octaves of abundance, shown in units of log (base 2). The log-normal distribution (for best fit curve, $\chi = 12.73$, $P > 0.05$) is given by $S_R = 8.0e^{-(0.158R)^2}$.

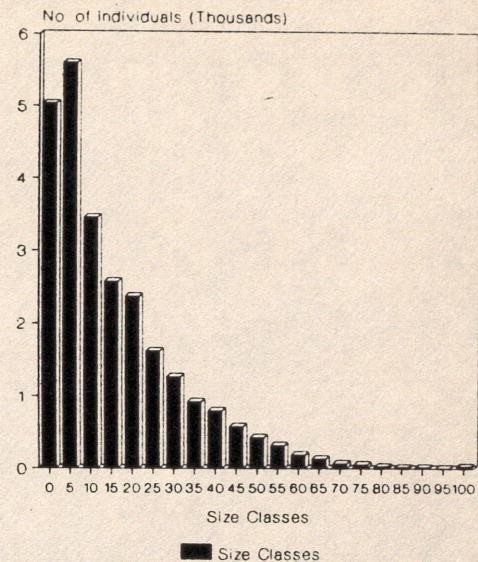


Figure 3. Size class (cm) frequency distribution of all the individuals in the plot (only the largest stem is considered for multiple-stemmed plants).

Table 2. Variance to mean ratio of density of species for varying plot sizes

Species	Plot size		
	1.00 ha	0.25 ha	0.04 ha
<i>Kydia calycina</i>	133.47	48.75	12.77
<i>Lagerstroemia microcarpa</i>	86.92	35.22	7.94
<i>Terminalia crenulata</i>	28.25	9.33	2.55
<i>Helicteres isora</i>	119.48	57.32	17.04
<i>Anogeissus latifolia</i>	39.73	14.74	3.77
<i>Tectona grandis</i>	8.50	3.40	1.44
<i>Cassia fistula</i>	17.39	7.47	3.03
<i>Xeromphis spinosa</i>	24.62	10.94	5.02
<i>Emblia officinalis</i>	4.04	2.16	1.25
<i>Grewia tiliifolia</i>	3.80	2.02	1.19
<i>Syzygium cumini</i>	6.25	2.56	1.47
<i>Shorea roxburghii</i>	28.56	9.09	3.72
<i>Bambusa arundinacea</i>	19.15	10.53	4.15
<i>Radermachera xylocarpa</i>	4.28	2.54	1.39
<i>Eriolaena quinquelocularis</i>	6.26	2.74	1.36
<i>Cordia obliqua</i>	4.61	2.43	1.33
<i>Diospyros montana</i>	4.89	2.10	1.48
<i>Stereospermum colias</i>	7.30	5.28	3.39
<i>Ougeinia oojeinensis</i>	16.92	9.04	2.95
<i>Lagerstroemia parviflora</i>	9.55	3.97	1.80
<i>Dalbergia latifolia</i>	4.16	2.51	1.70
<i>Cordia wallichii</i>	2.95	1.69	1.09
<i>Schleichera oleosa</i>	2.19	1.56	1.29
<i>Schrebera swietenoides</i>	6.61	3.12	1.58
<i>Terminalia chebula</i>	2.57	1.25	1.05
<i>Gmelina arborea</i>	1.30	1.13	1.09

Only species having 50 or more individuals in the 50-ha plot have been listed.

with a 'sufficient' time gap and not merely based on a one-time cross-sectional sampling.

Patterns of mortality

By far, the largest number of standing dead stems pertained to *Shorea roxburghii* (307 dead versus 79 living). Practically all living individuals were saplings, indicating there had been large-scale mortality of adult plants. The cause for this mortality seems to be an unidentified cerambycid beetle that is a stem borer. To investigate the population dynamics of *Shorea roxburghii*, we have also set up a one-hectare plot in Doddagatti Block of Mudumalai, where this species grows gregariously.

The data also indicated a high recent mortality of *Pterocarpus marsupium* (23 dead versus 22 living plants) and *Bridelia retusa* (17 dead, 40 living).

Patterns of species mortality should be more appropriately deduced from observing the community over a period of time and not from a one-time cross-sectional sampling. Dead stems of different species may be left standing for varying periods of time. Therefore an enumeration of standing dead stems may not reflect the true mortality pattern. Nevertheless, such an enumeration did provide useful hints as to what might have happened in the past.

The re-censuses carried out during 1989 and 1990 of the entire plot showed substantial decline in the total population. The decline was 9.1% during 1989 and 5.5% during 1990, or an overall decline of 14% from the base year. *Kydia calycina* and *Helicteres isora* showed the steepest decline, by 42% and 27% respectively, over the two-year period. This was largely

due to elephants stripping bark, breaking stems and pushing over trees and, to a lesser extent, due to fire (during 1989) killing the saplings.

Do we need a 50-hectare plot?

Criteria in selecting a plot size for studies of forest ecology have been more based on convention and convenience rather than on objective assessment of needs. The available resources and time obviously put a ceiling on the scale of operations. 'Favourite' plot sizes have been one hectare or a few hectares.

One objective criterion that has been used is based on species-area relationship. The smallest area that includes most if not all species in a community has been taken as the appropriate size for study. The species-area curve for the Mudumalai plot is shown in Figure 4.

The first hectare itself contains 31 species or 44% of the total species recorded. The range in species richness for a single hectare goes from a minimum of 19 to a maximum of 39 species. The number of species saturates by the 34th ha. In fact, with a plot size of 25 ha one would still have retained 63 or nearly 90% of the final species tally.

It is, however, obvious that given the distinctly clumped distribution of most species, a plot of one hectare would hardly be representative of the broader structure of the community. For instance, *Kydia calycina*, the most dominant species, was absent from a one-hectare subplot of the 50-ha plot, while *Lagerstroemia microcarpa*, the second most dominant, was missing from another one-hectare subplot. In many other hectares their densities vary enormously, from extremely low to extremely high, compared to their mean density over 50 ha. For instance, *Kydia calycina* has a density range of 0 to 607 individuals per hectare compared to its mean density of 104 individuals per hectare. In fact, in six hectares it is represented by only two individuals each and in 13 ha by less than 10 individuals each. In the case of *Lagerstroemia microcarpa* the range is 0-308 individuals per hectare, with a mean density of 80 ha⁻¹, and 16 ha having 20 or less individuals per hectare. It is easy then to imagine that even a plot of several hectares may not reflect the density levels of such clumped species in the community.

With a plot size of 25 ha the sample size for most species would be quite small. Only 19 species would be represented by over 50 individuals each. For the rest it would not be possible to do any kind of meaningful statistical analyses. With a 50 ha plot the situation is somewhat better with 26 out of 71 species having over 50 individuals each.

Even sample sizes of 50 would be insufficient for many kinds of statistical analyses. For instance, many species with abundances far in excess of 50 individuals are not adequately represented by different size classes,

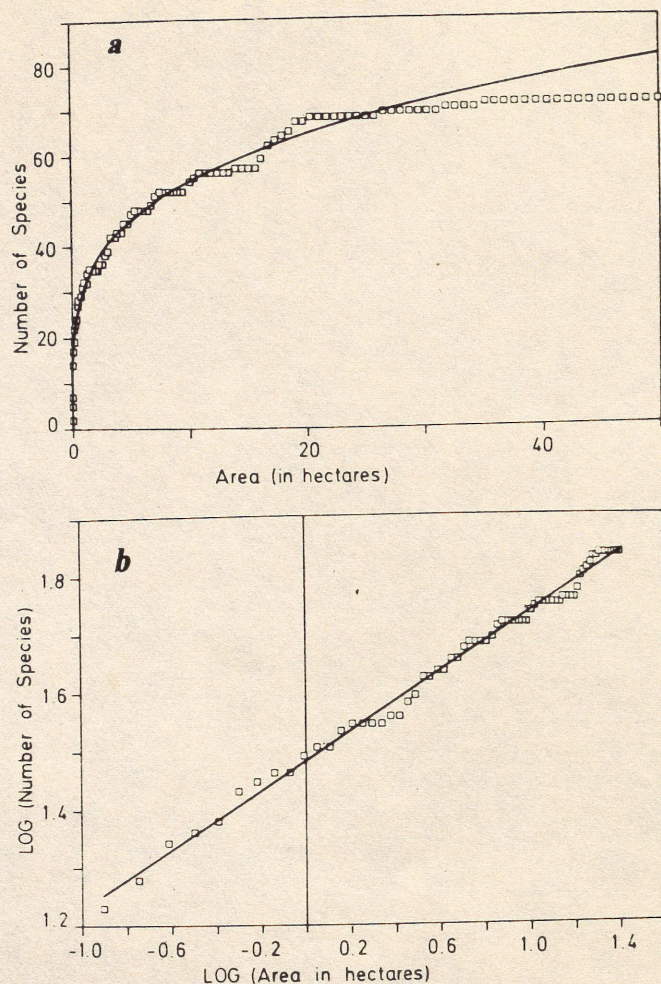


Figure 4. Species-area curve for the 50-ha plot shown on (a) a normal scale, (b) a \log_{10} - \log_{10} scale. The best fit regression for the log transformed data for 67 points (from 0.1 ha to 25 ha) is given by $\log(\text{number of species}) = 30 A^{0.25}$, where A is the area in hectares. The fitted curve for the normal data in (a) is based on the above regression. The expected number of species for the 50-ha plot is 81 species as opposed to only 71 species actually present.

that would permit a detailed insight into their life histories. From this consideration alone, we feel that a plot as large as 50 ha is justified.

Another important decision to make, while selecting plot size and shape, is whether to have a single large plot or a number of smaller plots spread over a larger tract but adding up to the same area. The answer would depend on the objectives of the study and one's definition of what constitutes an appropriate unit for studying a 'community'.

Several smaller plots distributed widely have the advantage of being able to potentially represent different 'vegetation types' and would probably encompass more species. Phenomena (say, massive mortality) that occur over a 50-ha scale may not be true when a larger spatial scale is considered; this may be better captured by studying several smaller plots. On the other hand, any individual plot may be still too small

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Table 3. Number of individuals retained and species lost for different minimum stem sizes

Smallest DBH measured (cm)	No. of individuals in sample	No. of species in sample	Species lost
1.0	25,929	71	—
2.0	23,835	69	<i>Buchanania axillaris</i> , <i>Cassia montana</i> .
3.0	22,807	67	Above plus <i>Grewia hirsuta</i> , <i>Crotalaria</i> sp.
5.0	20,898	66	Above plus <i>Dalbergia lanceolaria</i> .
10.0	15,417	63	Above plus <i>Indigofera cassioides</i> , <i>Allophylus cobbe</i> , <i>Pavetta tomentosa</i>

to make firm conclusions about community dynamics on a local scale. We plan to overcome this problem partly by setting up a series of smaller plots in addition to the large 50-ha plot.

A third decision to be made concerns the minimum cut-off size of plants to be included in the enumeration. Should this be 1 cm, 2 cm, 3 cm or 10 cm DBH? Traditionally, foresters have looked at only trees above 10 cm DBH (actually 30 cm girth). The resulting total individuals enumerated and the species lost for higher cut-off sizes are given in Table 3. With a 2 cm DBH cut-off only two species and just about 8% of individuals are lost from the sample. For 10 cm DBH and above the loss is much greater with eight species and 41% of individuals. The species lost are all from the rarer segment of the original sample.

The first impression might be that one could safely increase the cut-off size to 2 cm or 3 cm DBH without any significant loss in data (number of species and individuals). However, the opposite argument could be made that with only a marginally increased effort, one is able to capture the saplings of 1–2 cm DBH in the sample. Studying the patterns of recruitment of seedlings into the 1–2 cm DBH class and tracking their fate might be important for understanding the life histories of many plant species.

Conclusions

The 50-ha vegetation plot set up in Mudumalai Sanctuary offers an opportunity, unprecedented in this region, for a host of detailed studies on tropical forest biology. The fact that the precise locations of nearly 26,000 individuals, including saplings from 71 species, are known provides baseline data that can be of tremendous advantage for a variety of investigations. This could encompass the fields of reproductive ecology, population dynamics, community ecology, population genetics, plant productivity, applied silviculture and so on. Such investigations would hopefully

provide the scientific basis for sustainable management of tropical dry forests.

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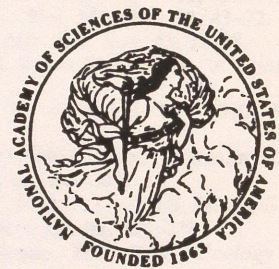
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On the relationship between bird and woody plant species diversity in the Uttara Kannada district of south India

(biodiversity/tropical forest)

R. J. RANJIT DANIELS*, N. V. JOSHI*, AND MADHAV GADGIL*†‡

*Centre for Ecological Sciences, †Jawaharlal Nehru Centre for Advanced Scientific Research, Indian Institute of Science, Bangalore 560012, Karnataka, India

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ABSTRACT Bird species richness is inversely related to woody plant species diversity and vertical stratification in the natural vegetation of Uttara Kannada, the district with the largest contiguous tract of humid tropical forest in peninsular India. This inverse relationship may be explained by the fact that although the peninsular Indian evergreen forests are rich in woody plant species when compared with the drier vegetation, they harbor an impoverished bird fauna due to their smaller overall extent and greater isolation. Much of this impoverishment is accounted for by the absence of many species of understory timaliids characteristic of the humid evergreen forests of the Eastern Himalayas and Southeast Asia. The plantations of Uttara Kannada largely derive their bird fauna from the drier vegetation and exhibit the commoner trend of a positive correlation between bird species richness and vertical stratification of the vegetation.

Conservation of biodiversity has emerged as a key environmental concern of the day. Effective action in this context calls for an understanding of how biodiversity is distributed and maintained, in particular, within the species-rich tropical forest regions that are being rapidly depleted. We have limited information on these issues, much of it from investigations in a few localities on only a few taxa. It would be useful to know how far we can generalize from this limited data base and to answer questions, such as whether or not localities rich in bird species are also rich in plant species and whether humid tropical forests are richer in the diversity of all major taxa they share with drier tropical forests.

Our investigation has been motivated by such questions. It assesses diversity levels in two of the best studied taxa of organisms—namely birds and angiosperm woody plants across a gradient of natural and man-made vegetation types. This work focuses on Uttara Kannada, a district harboring the most extensive contiguous tract of humid tropical forest in south India.

MATERIALS AND METHODS

The district of Uttara Kannada (13°55'–15°32'N; 74°05'–75°05'E) marks the transition between the more seasonal northern and the less seasonal southern Western Ghats. Humid evergreen dipterocarp forests reach their northern limits of distribution in this district, as do several species of vertebrates, including birds such as *Muscicapa pallipes*, *Pycnonotus priocephalus*, and *Dendrocitta leucogastra*. The district has a narrow coastal strip flanked by hills rising to 600–850 m before merging with the peninsular Indian plateau at an altitude of 500 m to the east. The annual rainfall varies from >3000 mm along the coast to 5000 mm along the crest of the hills, declining to 1000 mm on the east (Fig. 1). Much

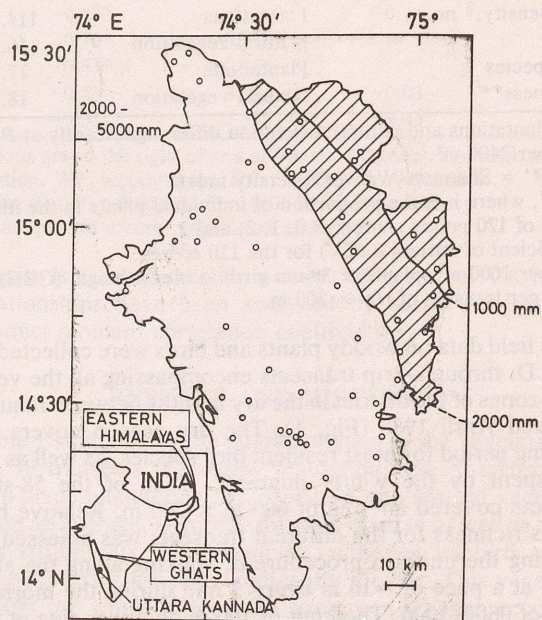


FIG. 1. Map of Uttara Kannada district showing major rainfall/vegetation zones and location of the 58 transects. ○, Transects; ▨, deciduous forest zone; □, evergreen/semideciduous forest zone.

of this rain is received during the monsoon months of June–October. Broad vegetation zones of the district correspond to this rainfall gradient. Evergreen forests with their secondary stages, which often include grass and thickets, dominate the coast and the western hill-slopes. Semideciduous and deciduous forests appear progressively eastward toward the plateau. Plantations, mostly monocultures of native as well as introduced tree species, including *Tectona grandis*, *Areca catechu*, *Eucalyptus*, *Casuarina equisetifolia*, *Acacia auriculiformis*, and *Anacardium occidentale*, form a patchwork throughout the forests of Uttara Kannada (1–3). These are extremely variable in age, structure, and composition (Table 1). Of these the betel nut (*A. catechu*) orchards are a traditional land-use system restricted to the evergreen forest zone and include many examples of mature plantations with a canopy in the range of 16–32 m. The *T. grandis*, *Acacia*, *Casuarina*, and *Eucalyptus* plantations have been raised in more recent times, and many of them represent young coppice growth.

Uttara Kannada with 60% of its 10,200 km² of land area covered by forests is not only the most forested district of the Western Ghats but also harbors the most diverse avifauna. A total of 403 species of birds have been reported from this district (4–7). Of these, 300 are land birds extensively using the forests. This bird fauna has changed but little over the past century in spite of many changes in land use (8).

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‡To whom reprint requests should be addressed.

Table 1. Attributes of natural vegetation ($n = 38$) and man-made plantations ($n = 20$) of the Uttara Kannada district

Attribute	Vegetation type	Mean	SD	Minimum	Maximum	Statistical significance
Woody plant species, no.*	Plantations	11.89	5.99	1.00	23.00	S
	Natural vegetation	40.58	13.76	17.00	64.00	
Woody plant species diversity [†]	Plantations	3.70	2.08	1.00	7.90	S
	Natural vegetation	15.52	7.57	2.50	32.70	
Vertical stratification [‡]	Plantations	3.26	1.24	1.50	5.69	S
	Natural vegetation	4.34	0.85	2.25	5.59	
Canopy density [§]	Plantations	1.23	0.57	0.26	2.21	S
	Natural vegetation	1.74	0.62	0.62	2.85	
CV of canopy density	Plantations	0.66	0.38	0.26	1.69	NS
	Natural vegetation	0.57	0.27	0.16	1.69	
Tree density, no.	Plantations	114.44	94.37	21.00	305.00	S
	Natural vegetation	56.87	23.99	23.00	119.000	
Bird species richness**	Plantations	17.33	4.84	10.00	31.00	NS
	Natural vegetation	18.66	7.10	4.00	31.00	

S, Plantations and natural vegetation differ significantly at $P < 0.01$; NS, not significant by t test.

*No. per 2400 m².

[†] $e^{H'}$, H' = Shannon-Weaver diversity index.

[‡] $1/\sum p_i^2$, where p is the proportion of individual plants in the i th height class.

[§]Mean of 120 points scored as 0, 1, 2, and 3.

^{||}Coefficient of variation (CV) for the 120 scores.

||No. per 1000 m²; plants \geq 30-cm girth at breast height (GBH).

**No. per transect of 600 \times 200 m.

The field data on woody plants and birds were collected by R.J.R.D. through strip transects encompassing all the vegetation zones of the district in the dry months between January 1986 and April 1988 (Fig. 1). The dry season covers the breeding period for most resident bird species, as well as the time spent by the winter migrants. Each of the 58-strip transects covered an area of 600 m \times 200 m. Relative bird species richness for the different transects was assessed by following the uniform procedure of walking along the strip center at a pace of \approx 10 m every 2 min during the morning hours of 0800–1000. The limit of 100 m on either side of the center line of the transects was fixed to allow for bird movement away from the observer and the range over which birds may be heard (9, 10). Birds were recorded as those sighted and/or heard on the transect, heard in the background apparently beyond transect limits, and flying overhead. This count was supplemented by more extensive, albeit less standardized, recording of all occurrences of bird species in the different vegetation zones of the district. Comparison of the more complete estimates of the bird species richness thus made with the transect estimates suggests that the birds recorded on the transect during the 2-hr sampling represent 30–40% of the total bird species in a locality. Species numbers estimated through recording those flying overhead and heard in the background were a more variable fraction of

the total. Furthermore, the vegetation of Uttara Kannada is highly patchy, and the birds thus heard in the background beyond transect limits or flying overhead often represent habitat types other than those on the transect. Hence, all further analysis is based on the species of birds directly recorded (seen or heard) on the transect.

The transects covered two broad categories of vegetation—namely, natural forests and man-made plantations. The vegetation was characterized by the following attributes: species richness and abundance of woody plants, vertical stratification, extent of canopy cover, and tree [\geq 30 cm girth at breast height (GBH)] density. The woody plants were surveyed along a strip of 4-m width defined by using nylon ropes along the center of the transect on which birds were sampled. All individuals were identified and assigned to one of the following seven height classes: 0–1 m (seedlings), 1–2 m (shrubs), 2–4 m (understory), and the several canopy layers at 4–8 m, 8–16 m, 16–32 m, and $>$ 32 m. Vertical stratification in the present study thus reflects the proportion of woody plants in each height class rather than the amount of foliage, as is the case with the index of foliage height diversity introduced by MacArthur and MacArthur (11). The extent of canopy density at any point was scored as 0 when there was none overhead, 1 when canopies from adjacent trees barely met, 2 when the canopies overlapped with the

Table 2. Attributes of natural vegetation and associated bird species along a gradient of decreased moisture in the Uttara Kannada district

Attribute	Count, mean \pm SD			Statistical significance		
	Evergreen ($n = 20$)	Semideciduous ($n = 9$)	Deciduous ($n = 9$)	E-S	E-D	S-D
Woody plant species	50.3 \pm 5.97	36.33 \pm 13.16	23.22 \pm 4.2	S*	S*	S [†]
Woody plant species diversity	18.86 \pm 6.47	15.33 \pm 8.39	8.3 \pm 1.38	NS	S*	S [†]
Vertical stratification	4.73 \pm 0.66	4.02 \pm 0.77	3.77 \pm 0.83	S [†]	S*	NS
Canopy density	2.15 \pm 0.55	1.31 \pm 0.33	1.26 \pm 0.191	S*	S*	NS
CV of canopy density	0.52 \pm 0.34	0.67 \pm 0.15	0.58 \pm 0.78	NS	NS	NS
Tree density	68.7 \pm 24.67	45.67 \pm 16.35	41.78 \pm 12.04	S [†]	S*	NS
Percentage deciduous [‡]	9.0 \pm 5.4%	38.3 \pm 10.0%	61.4 \pm 9.3%	S*	S*	S*
Bird species richness	17.8 \pm 6.90	18.78 \pm 7.39	20.44 \pm 6.88	NS	NS	NS

E-S, evergreen – semideciduous; E-D, evergreen – deciduous; S-D, semideciduous – deciduous; CV, coefficient of variation; S, significant; NS, not significant.

* $P < 0.01$.

[†] $P < 0.05$.

[‡]Percentage of total number of woody plant species.

Table 3. Correlation matrix of attributes of 38 samples of natural vegetation and 20 samples of plantations in the Uttara Kannada district

	WP species richness	WP species diversity	Vertical stratification	Canopy density	CV of canopy density	Tree density	Bird species richness
WP species richness		0.78*	-0.09	0.37	0.48	-0.25	0.39
WP species diversity	0.83*	0.73*	0.28	0.53*	0.57*	0.06	0.17
Vertical stratification	0.51†	0.67*	0.49	-0.39	-0.53	0.04	-0.38
Canopy density	0.85*		-0.09	-0.14	-0.29	-0.06	-0.35†
CV of canopy density	0.52*	0.44*		-0.09	0.08	0.33	0.49‡
Tree density	-0.45	-0.42	-0.27	0.00	-0.27	-0.06	-0.24‡
Bird species richness	0.70*	0.62*	0.56*		-0.84*	0.68*	-0.28
	0.34	0.16	0.17	-0.83*	-0.64*	0.46*	0.15
	-0.31	-0.37†	-0.49*	-0.77*		0.37	-0.24
	-0.45	-0.40	-0.08	0.76*	0.51†	-0.14	0.07
	0.56*	0.49*	0.45*	0.83*	-0.69*		0.22
	0.37‡	0.29‡	0.54†‡	-0.23	0.18	-0.03	-0.28
	-0.31‡	-0.44*‡	-0.39†‡	-0.36†	0.37†	-0.43*	

Simple correlations are to the left of and below the diagonal; partial correlations are to the right of and above the diagonal. For each attribute the upper row refers to plantations, and the lower row refers to natural vegetation. WP, woody plant; CV, coefficient of variation. * and †Values of simple/partial correlation coefficients differ significantly from 0 at $P < 0.01$ and $P < 0.05$ level, respectively. ‡Values of simple/partial correlation coefficients differ significantly for plantations and natural vegetation at $P < 0.05$.

sky still showing through, and 3 when the sky was no longer visible through the overhead leaves. A total of 120 points at 5-m interval was scored in this way over the entire length of each transect. Tree density was estimated by using 10 m × 10 m quadrants. Ten quadrants (five on either side) were laid along the central line of the strip transects at intervals of 50 m, and all trees were counted.

Woody plant species diversity is computed as $e^{H'}$, where H' is the Shannon-Weaver index $-\sum p_i \ln p_i$, and p_i is the proportion of plants belonging to the i th species. Vertical stratification is computed by using the reciprocal Simpson index $1/\sum p_i^2$, where p_i is the proportion of woody plant individuals in the i th height class. Canopy cover has been estimated by averaging the density scores. The coefficient of variation in the canopy density is a measure of the extent of heterogeneity in the canopy cover over the transects. Tree

density is expressed as the number of trees per 1000 m². All relationships have been analyzed by using the Pearson's product moment correlation coefficient r .

RESULTS AND DISCUSSION

Table 1 summarizes the characteristics of the vegetation for the 38 transects in natural vegetation and 20 transects in man-made plantations. As expected, the natural vegetation is, on an average, significantly more diverse as well as denser and structurally more complex, although its bird species richness levels are not significantly greater. This vegetation covers the whole range from evergreen through secondary evergreen, semideciduous, and deciduous types, with an increased proportion of deciduous species and decreased levels of woody plant species richness, density, and stratification as one progresses eastward to drier tracts (Table 2).

Our first notable result is that for natural vegetation, bird species richness significantly correlated negatively with woody plant species diversity as well as with vertical stratification, canopy density, and tree density. Bird species richness is, however, significantly correlated positively with the coefficient of variation of canopy density, suggesting that bird species richness increases with patchiness of tree cover

Table 4. Comparison of the number of species of humid evergreen forest birds of selected families in Western Ghats and Eastern Himalayas

Family	Exclusive to Western Ghats	Exclusive to Eastern Himalayas	Shared by both	Remarks
Phasianidae	1	6	0	Large ground bird
Columbidae	1	6	5	Large arboreal frugivore
Trogonidae	1	2	0	Large arboreal insectivore
Bucerotidae	2	4	1	Large arboreal frugivore
Capitonidae	2	4	0	Medium-sized frugivore
Picidae	1	6	5	Small-large insectivore
Corvidae	1	3	0	Large omnivore
Pycnonotidae	2	5	2	Medium-sized frugivore
Muscicapidae: Timaliinae	4	56	4	Sedentary insectivore
Total	15	92	17	

These data are from Ali and Ripley (19).

Table 5. Comparison of number of species of birds characteristic of drier habitats in Southeast Asia and adjoining tracts of Eastern Himalayas and the rest of the Indian subcontinent

Family/genera*	Southeast Asia/Eastern Himalayas	Indian subcontinent
Otitidae	2	6
Cursoridae	0	3
Alaudidae		
(<i>Erimopterix</i> , <i>Ammomanes</i> , <i>Galerida</i>)	1	7
Ploceidae (<i>Estrilda</i> , <i>Ploceus</i> , <i>Lonchura</i>)	11	11
Phasianidae		
(<i>Francolinus</i> , <i>Galloperdix</i> , <i>Perdica</i>)	4	11

These data are from Ali and Ripley (19) and King and Dickinson (20).

*The genera have been separately indicated where the entire family is not considered.

Table 6. Habitat preference of the birds as percentage of species found in the different kinds of vegetation of the Uttara Kannada district

Birds	Habitat				
	Evergreen forest	Deciduous forest	Teak plantation	Eucalyptus plantation	Betel nut plantation
Closed forest specialist	77.27	40.91	37.03	4.76	35.29
Open forest specialist		9.1	14.81	19.05	11.76
Generalist using several habitats	22.73	50.00	48.15	76.19	52.94

These data are from Daniels *et al.* (3).

and presence of treefall gaps (12). Table 3 shows that the various attributes of natural vegetation strongly correlate with each other. Hence, we performed a partial correlation analysis to determine the relative significance of different vegetational attributes by excluding the effect of other attributes with the path analysis technique (13). This analysis reveals that the predominant influence is that of tree species diversity: the more diverse natural vegetation supports a significantly lower number of bird species.

The second notable result is that the man-made plantations differ from natural vegetation in this regard. In these plantations bird species richness correlates positively with stratification. Furthermore, the levels of positive correlations for plantations between bird species richness and woody plant species richness and woody plant species diversity significantly differ from the negative correlations obtained for the natural vegetation. As for natural vegetation, woody plant species richness, diversity, and vertical stratification positively correlate among themselves, whereas the mean of canopy density negatively correlates with its coefficient of variation.

The biota of Uttara Kannada district, thus, exhibits two trends that are more widely known and one that is only occasional. (i) The first, near universal trend is that of increase in plant species diversity coupled with greater levels of vertical stratification along the gradient of increased availability of moisture in the natural vegetation. In the tropical latitudes the proportion of evergreen plant species increases along the same gradient, so that the moister forest vegetation dominated by evergreen plants is more stratified and richer in woody plant species (Table 2). (ii) Bird species diversity is generally positively correlated with woody plant species diversity and/or stratification (11, 14, 15). (iii) This trend holds for the plantations of Uttara Kannada but is reversed for the natural vegetation, so that the more stratified and diverse evergreen forest vegetation harbors fewer bird species compared with the less stratified and less diverse deciduous vegetation of drier tracts.

The explanation for the lower level of bird species richness in the structurally more complex and diverse vegetation could lie in the smaller size of the potential pool of colonizers for such vegetation. Indeed, such an effect has been noted

both for continental (Patagonia in South America) and island (West Indies) bird faunas (16, 17). We might, therefore, expect that the bird fauna of evergreen forests of Uttara Kannada derives from a smaller pool of potential colonizers in comparison with the drier forests. This prediction is related to the fact that the evergreen forests of Uttara Kannada are part of the evergreen forest vegetation of the Western Ghats, constituting a relatively restricted habitat island (64,750 km²) at a great distance (1500 km) from the larger contiguous tract of evergreen vegetation in the Eastern Himalayas and South-east Asia. On the other hand, the deciduous forest vegetation of Uttara Kannada is part of and contiguous with the large tract of deciduous and scrub vegetation (2,774,850 km²) that covers most of the Indian subcontinent (18).

The bird fauna of the Western Ghats is, indeed, impoverished, especially with respect to land birds in comparison with the Eastern Himalayas, although the latter region is slightly smaller in area (19, 20). Thus, Western Ghats harbor a total of 507 species, of which 363 are land birds, while the Eastern Himalayas harbor 536 species, 523 of which are land birds. Table 4 further compares these two bird faunas with respect to families particularly characteristic of humid forests. This count leaves out bird species characteristic of altitudes >2500 m because the Western Ghats are almost entirely confined to lower elevations. Such a comparison reveals that larger sized birds, frugivores, and, above all, sedentary insectivores belonging to the subfamily Timaliinae are very poorly represented on the Western Ghats. In fact, Western Ghats harbor only 200 species characteristic of evergreen forests. This impoverishment is analogous to that noted by Terborgh and Winter (21), who conclude that members of families Phasianidae, Picidae, Timaliinae, and Bucerotidae are especially prone to extinction on land-bridge islands. We have no evidence as to whether members of these families never reached the Western Ghats or became extinct subsequently, perhaps with shrinkage in overall area of the evergreen forest tracts after reduction in rainfall. It is, nevertheless, likely that members of Timaliinae (babblers and laughing thrushes), being highly sedentary, territorial, and social birds, are very poor dispersers and may have never reached the Western Ghats.

Table 7. Food preferences of birds as percentages of species in the different kinds of vegetation of the Uttara Kannada district

Food preference	Vegetation				
	Evergreen forest	Deciduous forest	Teak plantation	Eucalyptus plantation	Betel nut plantation
Predominantly frugivores	45.45	22.73	22.22	14.29	5.88
Predominantly insectivores	50.00	59.09	62.96	71.43	76.47
Predominantly herbivores	4.55	13.64	11.11	9.52	11.76
Omnivores	0.00	0.00	3.70	4.76	5.88

These data are from Daniels *et al.* (3).

Although the evergreen forests of Western Ghats are thus impoverished of birds characteristic of humid forests, the Indian subcontinent is rich in birds characteristic of drier vegetation. This fact is emphasized in Table 5, which compares the number of species in selected genera and families for the Indian subcontinent (excluding Eastern Himalayas) with Southeast Asia along with the adjacent Eastern Himalayas—the two tracts having areas of comparable extent (19, 20). The size of species pool of drier forests, scrub, and secondary vegetation of peninsular India exceeds 275, substantially larger than the species pool of 200 characteristic of evergreen forests of Western Ghats (19). Hence, the evergreen forest avifauna of Uttara Kannada, subject to lower immigration pressure, may have coadapted to be saturated at a relatively low level of species richness when compared with that of drier tracts, subject to immigration pressure from a larger species pool. This fact could account for the inverse relationship between bird species richness and woody plant species diversity or stratification in the natural vegetation of Uttara Kannada.

In an earlier study from the same district (3), plantations were shown to exhibit levels of bird species richness not significantly different from those of the natural forests. The bird communities of plantations of Uttara Kannada closely resemble those of the drier forest tracts (Tables 6 and 7). This result is to be expected because plantations are closer to the deciduous forests in the scarcity of plant species bearing fleshy fruits, in their relatively simple structure, and in their low woody plant species diversity. Sharing the richer bird species pool with deciduous forests, the plantations exhibit the commoner trend of an increase in bird species richness with greater stratification of the woody vegetation.

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type pollens, while the (N, N) flowers will be fertilized by at most one S-type pollen, the other one always being type N. In other words, frequencies of (NS, NS), (NS, SS) and (SS, SS) fruits obtained by pollination by two S-type pollens will be vanishingly small and hence can be neglected in the first-order approximation.

Thus, the frequency of (NN, NS) fruits

$$\begin{aligned} &= y(1 - y)/2 \quad (\text{from (N, S) type of flowers fertilized by N-type pollen}) \\ &\quad + (y/2) \cdot 2(1 - y) \quad (\text{from (N, N) flowers fertilized by one N and one S pollen}) \\ &= 1.5y, \end{aligned}$$

and the fitness of the (NS) seed is $1 + b$.

On the other hand, the frequency of the (NS, NS) fruits

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Sibling rivalry between seeds within a fruit: Some population genetic models*

N. V. JOSHI

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

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Abstract. Competition between seeds within a fruit for parental resources is described using one-locus-two-allele models. While a “normal” allele leads to an equitable distribution of resources between seeds (a situation which also corresponds to the parental optimum), the “selfish” allele is assumed to cause the seed carrying it to usurp a higher proportion of the resources. The outcome of competition between “selfish” alleles is also assumed to lead to an asymmetric distribution of resources, the “winner” being chosen randomly. Conditions for the spread of an initially rare selfish allele and the optimal resource allocation corresponding to the evolutionarily stable strategy, derived for species with n -seeded fruits, are in accordance with expectations based on Hamilton’s inclusive fitness criteria. Competition between seeds is seen to be most intense when there are only two seeds, and decreases with increasing number of seeds, suggesting that two-seeded fruits would be rarer than one-seeded or many-seeded ones. Available data from a large number of plant species are consistent with this prediction of the model.

Keywords. Intra-brood conflict; sibling rivalry; brood reduction; cannibalism; seed–seed competition; evolutionarily stable strategy.

1. Introduction

Like many of Haldane’s other contributions to population genetics, his model of family level selection (Haldane 1924) also has a much broader range of applications. By comparing the rate of increase of the frequency of the allele favoured by natural selection when competition between individuals was population-wide to the rate when competition was restricted to members of the same family, Haldane demonstrated that the process of family level selection was relatively slower, almost by a factor of two (Haldane 1924; Sutter 1968). However, the formalism developed by him is ideally suited for modelling evolutionary processes that in fact operate at the level of the family, e.g. parent–offspring interactions and sibling rivalry. In this paper, the evolution of sibling rivalry in plants is investigated using methods similar to Haldane’s family-level (familial) selection models.

In many bird species, there is an intense and often violent competition between chicks in the same clutch for the food brought by the parents. Indeed, earlier models that described sibling rivalry were inspired by bird species (O’Connor 1978; Stinson 1979), though more general models had also been formulated (Macnair and Parker 1979). It was quickly realized, however, that competition among seeds in a fruit is an equally valid example of intra-brood conflict, is equally intense, and can be described by similar models (Nakamura 1980; Kress 1981). Inclusive fitness models (Westoby

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and Rice 1982; Queller 1983) as well as genetic models (Law and Cannings 1984) have been used to examine the various details of this phenomenon. Uma Shaanker *et al.* (1988), in addition to presenting a broad review of brood size patterns in plants, have developed models describing parent-offspring as well as offspring-offspring conflict. Lovett Doust and Lovett Doust (1988) view these processes from an even broader view, that of plant reproductive strategies.

While the present investigation draws on the earlier studies, it differs from them in simultaneously considering (a) an explicit population genetic model for n -seeded fruits, using the fitness function commonly used for plant systems; (b) an asymmetric outcome of competition between identical genotypes; (c) separate and explicit conditions for the spread of the selfish allele and for the evolutionarily stable strategy (ESS); and (d) the relative rarity of two-ovuled plant species, and offering a possible explanation for it.

2. The model

An infinite, panmictic population of a purely cross-pollinating species with nonoverlapping generations is considered, with selection operating on two alleles—the recessive normal (N) and the dominant selfish (S). The situation where there are two seeds per fruit is described in detail here, while generalization to n -seeded fruits is developed in the appendix.

2.1 Competition between seeds

Since there are two seeds per fruit, and there are two phenotypes of seeds (normal and selfish), there will be three types of fruits:

- (i) In a fruit with both seeds of the normal type, resource is assumed to be shared equally, and the fitness of each seed is assumed to be unity.
- (ii) In a fruit with one selfish seed and one normal seed, the selfish one acquires a higher share of resources from the maternal parent, and thereby acquires a fitness of $1 + b$ (where b , the benefit, > 0). The normal seed, which consequently gets a reduced level of resource, obtains a fitness of $1 - c$ (where c , the cost, > 0).
- (iii) In a fruit where both the seeds are selfish, either of them is likely (with equal probability) to acquire a larger share of resource. This could be, for example, because one of the ovules is fertilized earlier than the other, or is closer to the resources (see Lee (1988) for a review). Each one thus obtains fitness $1 + b$ or $1 - c$ with a probability of half.

2.2 Spread of the selfish allele S

Let y (≈ 0) be the frequency of NS heterozygotes (and $1 - y$, the frequency of NN homozygotes). This implies the frequency of pollen of haplotype S to be $y/2$.

The NS heterozygote maternal parents would develop three types of two-ovuled flowers, (N, N), (N, S) and (S, S) (where N and S denote the haploid state of the egg within the ovule) in the proportion 0.25:0.5:0.25. The frequency of flowers containing an S-type ovule, and the frequency of the S-type pollen, are both very small (of order

y); and in the first-order approximation, terms of order y^2 can be neglected. This means that flowers containing S-type ovules (one or two) will be fertilized only by N-type pollens, while the (N, N) flowers will be fertilized by at most one S-type pollen, the other one always being type N. In other words, frequencies of (NS, NS), (NS, SS) and (SS, SS) fruits obtained by pollination by two S-type pollens will be vanishingly small and hence can be neglected in the first-order approximation.

Thus, the frequency of (NN, NS) fruits

$$\begin{aligned} &= y(1-y)/2 \quad (\text{from (N, S) type of flowers fertilized by N-type pollen}) \\ &\quad + (y/2) \cdot 2(1-y) \quad (\text{from (N, N) flowers fertilized by one N and one S pollen}) \\ &= 1.5y, \end{aligned}$$

and the fitness of the (NS) seed is $1+b$.

On the other hand, the frequency of the (NS, NS) fruits

$$= y(1-y)/4 \quad (\text{from the (S, S) types of flowers fertilized by N-type pollen})$$

and the fitness of each NS seed is $1+(b-c)/2$, and the net contribution of the two seeds is $2+b-c$. Hence the frequency of NS in the next generation, y' , is given by

$$\begin{aligned} y' &= [1.5y(1+b) + 0.25y(2+b-c)]/2 \\ &= y(1+(7b-c)/8). \end{aligned}$$

The allele S will increase in population if $y' > y$, i.e. if $(7b-c)/8$ is a positive quantity, i.e. if $7b > c$.

The condition for the spread of the selfish allele thus turns out to be

$$b > c/7,$$

where b and c denote benefit to the usurper and cost to the other seed, as described earlier.

2.3 Evolutionarily stable strategy

Consider now competition between two selfish alleles, the recessive S which leads to benefit b and cost c and the dominant S' which leads to benefit b' and cost c' .

Clearly, the fitness of an SS seed from an (SS, SS) fruit would be $1+(b-c)/2$ as described earlier, while that of an SS' seed from an (SS', SS') fruit would be $1+(b'-c')/2$. For an (SS, SS') fruit, the probability of SS' being the winner is 0.5, which gives it a fitness of $1+b'$. On the other hand, the probability of SS being the winner is also 0.5, whence the loser SS' obtains a fitness of $1-c$. The fitness of the SS' seed in an (SS, SS') fruit is thus $1+(b'-c)/2$.

As before, assuming z to be the frequency of SS' heterozygotes, $1-z$ the frequency of SS homozygotes, and $z/2$ the frequency of S' pollen, the average fitness of SS' is given by

$$\begin{aligned} &[1.5z(1+(b'-c)/2) + 0.25z(2+b'-c)]/z \\ &= 2+b'-3c/4-c'/4 \end{aligned}$$

On the other hand, fitness of SS is $2+b-c$. For S' to be able to invade the S

population

$$2 + b' - 3c/4 - c'/4 > 2 + b - c,$$

$$\text{i.e. } b' - c'/4 > b - c/4.$$

In other words, a strategy corresponding to the resource allocation that maximizes $b - c/4$ will be able to invade any other strategy corresponding to a different allocation and in turn will be uninvadable by any other strategy. Thus the allocation which maximizes $b - c/4$ is the evolutionarily stable strategy (ESS).

The pollen that fertilize the two ovules in the flowers are assumed to come from different plants. The two seeds in the fruit are, therefore, half-sibs (same mother, different father), and the coefficient of relatedness between the two seeds is therefore 0.25. The quantity $b - c/4$ thus turns out to be the change in the inclusive fitness (Hamilton 1964) of the dominant seed. The ESS is thus the one that maximizes the change in the inclusive fitness, which in the present situation is the same as maximizing inclusive fitness itself.

2.4 Resource-fitness relationship

For a seed to be viable, a minimum threshold level of resource must be invested in it. Thereafter, the increase in fitness (or survival) of the seed with increasing investment of resource obeys the law of diminishing marginal returns. The functional form

$$\text{fitness} \propto (R - R_{\min})^x,$$

where

$$0 < x < 1,$$

is normally used to describe such a relationship in plants (Smith and Fretwell 1974). In this expression, the power x indicates the efficiency of the seed in converting resources into fitness; thus a higher value of x corresponds to a higher level of efficiency. Without loss of generality, R_{\min} can be assumed to be unity. The optimal parental investment per seed can then be shown to be equal to $1/(1-x)$ (see, for example, Ganeshaiah *et al.* 1991).

In the present model, it is assumed that the parental allocation of resources to a fruit is in accordance with the optimal investment per seed. Thus, a two-seeded fruit obtains an investment of $2/(1-x)$. This is then split between the two seeds according to their competitive ability. It is further assumed that the value of x is the same for all the genotypes, i.e. the efficiency of the selfish seed in converting the higher share of resources obtained by it into fitness is assumed to be the same as that of a normal seed.

When the investments are equal, each seed obtains a fitness

$$F = \left(\frac{1}{1-x} - 1 \right)^x. \quad (1)$$

Let f be the fraction of the total resource obtained by the selfish phenotype ($f > 1/2$). Its fitness is then given by

$$F' = \left(\frac{2f}{1-x} - 1 \right)^x. \quad (2)$$

The remaining resource is invested in the other seed, and its fitness is given by

$$F'' = \left(\frac{2(1-f)}{1-x} - 1 \right)^x \quad (3)$$

Since the fitness of the selfish seed is $1 + b$ and that of the seed with lower resource is $1 - c$, relative to the fitness of the normal seed in a (NN, NN) fruit, the expressions for benefit and cost turn out to be

$$b = F'/F - 1$$

and

$$c = 1 - F''/F.$$

It should be borne in mind that, should the level of investment in a seed fall below unity, it does not survive, and the cost becomes equal to 1, regardless of the actual level of investment.

Using equations (1), (2) and (3), for a given value of x it is possible to compute the values of b and c for any level of usurpation f shown by the selfish allele. Since f can vary between $1/2$ (equal investment) and 1 (all the resource garnered by the selfish allele), it is possible to obtain the range of f values (for a given value of x) where $b > c/7$, i.e. where the selfish allele can invade the population of normal allele.

Similarly, it is possible to obtain the ESS in terms of f , for a given value of x . It is seen that maximization of $b - c/4$ is equivalent to

the maximization of $\frac{F'}{F} - 1 - (1 - F''/F)/4$,

i.e. maximization of $(F' + F''/4)/F$,

i.e. maximization of $4F' + F''$ with respect to f .

It is seen that the value of f corresponding to this optimum, \hat{f} , is given by

$$\hat{f} = \frac{1}{2} + \frac{1}{2} \left[\frac{x(1 - 4^{1/(x-1)})}{1 + 4^{1/(x-1)}} \right] \quad (4)$$

Let \hat{I} be the value of $b - c/4$ obtained corresponding to \hat{f} . When all the resource is garnered by the selfish seed, i.e. when $f = 1$, then $c = 1$, and let I^* be the corresponding value of $b - c/4$. Using this notation, if $I^* > \hat{I}$, then $f = 1$ will be the ESS.

3. Results and discussion

3.1 Spread of the selfish allele

The population genetic model described above for two-seeded fruits indicates that a selfish allele would spread in the population if $b > c/7$. Since the coefficient of relatedness between two seeds is 0.25 (section 2.3), it might seem that Hamilton's (1964) inequality would suggest the condition to be $b > c/4$. However, the outcomes of competition between related and unrelated seeds are different; a selfish seed is assumed to always outcompete a normal (not carrying the S allele, hence unrelated) seed, thereby obtaining a fitness b . It is only when the competitor is between two selfish (carrying S, hence related) seeds that a non-zero cost is encountered. When

the probabilities of occurrence of these two situations are taken into account (as in the derivation), the condition $b > c/7$ is obtained. The tolerance of the higher cost is thus due to a higher probability of benefit being accrued from competition against a normal (hence unrelated) seed.

As seen from the appendix (A1), the condition for the spread of the selfish allele in species containing n seeds per fruit is given by

$$b > c \left[\frac{(n-2)2^{n-1} + 1}{(n+2)2^{n-1} - 1} \right].$$

Thus, for example, for three-seeded and four-seeded fruits, the conditions for the spread of the selfish allele are $b > 5c/19$ and $b > 17c/47$ respectively. The spread of selfishness thus seems to become less likely as the brood size increases (figure 1), as expected.

The conditions obtained above can be used to investigate the evolution of brood reduction. If the entire resource is acquired by the dominant seed (or if the quantity of resource available for the other seeds is less than one unit per seed), only the dominant seed survives, and the others are aborted. When one examines the dynamics of the spread of such an excessively selfish allele (the brood reducer, i.e. the one which usurps the entire resource) for different values of x , the exponent of the fitness function, it is seen that for values of $x < 0.041$, b cannot be more than $c/7$. This is intuitively reasonable, as low values of x correspond to low efficiency of conversion of resources into fitness. For lower values of x , the increase in fitness obtained by acquiring additional resource is not commensurate with the loss in fitness due to the loss of siblings.

The critical values of x (i.e. those values below which the brood reducer allele cannot successfully invade a population of normal alleles) for three-seeded and four-seeded species (obtained using the methods described in section 2.4) are 0.068 and 0.086 respectively, and increase with n , the number of seeds in a fruit (figure 2), for low values of n , further highlighting the constraints imposed on the extent of sibling rivalry by higher seed numbers.

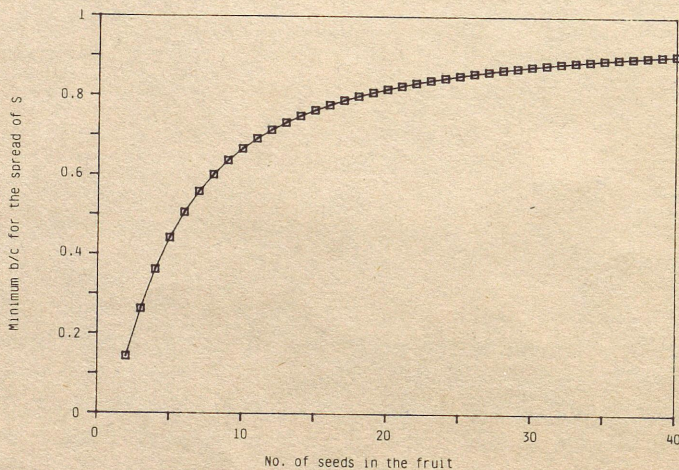


Figure 1. The threshold of b/c that has to be exceeded for a selfish allele to spread in the population as a function of n , the number of seeds in a fruit.

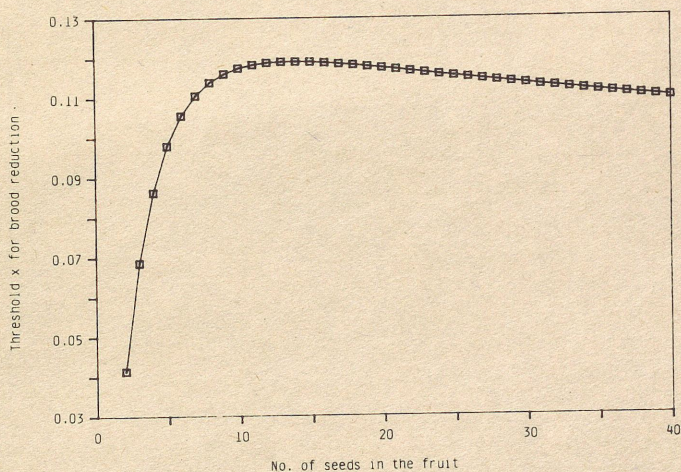


Figure 2. The critical value of x (the exponent in the fitness function, indicative of the efficiency of conversion of resource into fitness), below which a brood reducing allele (i.e. the one that acquires the entire resource for itself, thereby leading to the death or abortion of the rest of the seeds in the fruit) cannot spread in a population (of normal, N -type alleles), as a function of n , the number of seeds in a fruit.

For higher values of n (beginning with $n = 15$), the critical value of x starts decreasing with increasing n (figure 2), though rather slowly. The reason for this lies in the functional dependence of b , c , and the threshold of b/c necessary for the spread of the selfish allele on n , the number of seeds in a fruit. The benefit b increases slowly, but steadily, with n . The cost c is always equal to unity, since seeds other than the dominant one do not survive. The threshold increases rapidly with n initially, but is constrained to reach a value of unity asymptotically. As a result, for low values of n , the rate of increase of the realized value of b/c is lower compared to the rate of increase of the threshold with increasing n . Consequently, higher values of x are needed for brood reduction to evolve as n increases in the initial stages ($n = 2$ to 14). Beyond this range, however, while the benefit continues to increase, the increase in the threshold is negligible. Hence, smaller values of x are adequate to enable b/c to exceed the threshold. The critical value of x necessary for the brood reducing allele to spread thus starts decreasing with increasing n . However, one of the assumptions of the model, viz. that the rest of $n - 1$ seeds (i.e. those other than the dominant one) obtain an identical share of the remaining resource, would be quite unrealistic in such a situation. The consequences of using different, more appropriate forms of resource allocation are being investigated.

3.2 Evolutionarily stable strategy

For two-seeded species, the optimal fraction \hat{f} of the resource, acquired by the seed with the selfish phenotype (i.e. the value which makes the corresponding allele uninvadable), is equal to 0.5 for $x \approx 0$ and increases with x , reaching $\hat{f} = 1$ as x reaches unity. However, this optimum (in the sense of maximization of $b - c/4$) is only a local one. For $x > 0.1017$, it turns out that $\hat{f} = 1$ is the ESS.

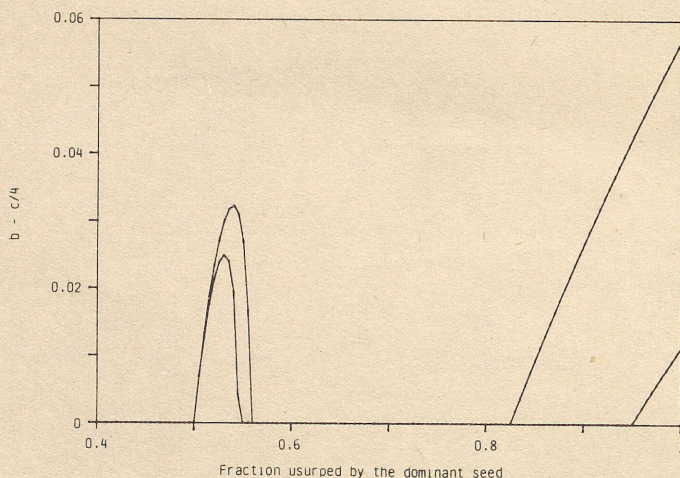


Figure 3. The value of $b - c/4$ as a function of f , the fraction of the resource usurped by the dominant seed, for two different values of x . The lower (and inner) curve corresponds to $x = 0.095$, while the upper (and outer) curve corresponds to $x = 0.12$.

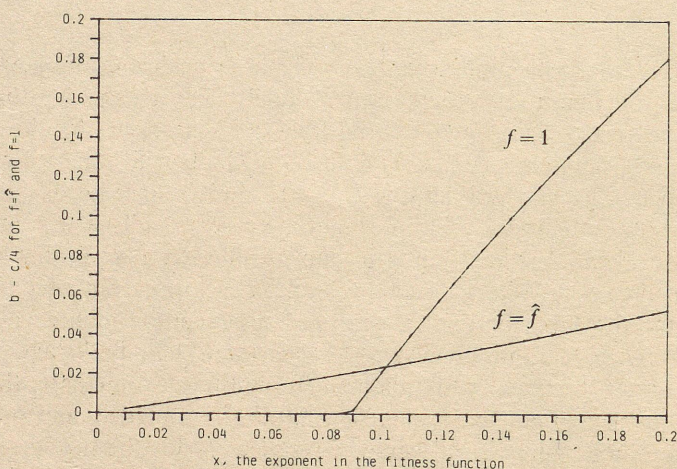


Figure 4. The value of $b - c/4$ at \hat{f} , the optimum fraction, as a function of x for two-seeded fruits. The value of $b - c/4$ when $f = 1$ (where all the resource is usurped by the dominant seed), also shown in the diagram, is below the former for $x < 0.1017$ and above it for higher values of x .

This can be better understood from figure 3, which shows the variation of $b - c/4$ as a function of f , the fraction usurped by the dominant seed, for $x = 0.095$. Clearly, $f = 0.5376$ is the ESS. On the other hand, for $x = 0.12$ (figure 3), even though $f = 0.5482$ corresponds to a maximum, the value of $b - c/4$ at $f = 1$ is higher than that, indicating $f = 1$ to be the ESS. As seen from figure 4, the value of $b - c/4$ at \hat{f} is above that corresponding to $f = 1$ for values of $x < 0.1017$, and is below it for higher values of x . In other words, for $x > 0.1017$, the ESS corresponds to the entire resource being acquired by the selfish seed, thereby leading to brood reduction.

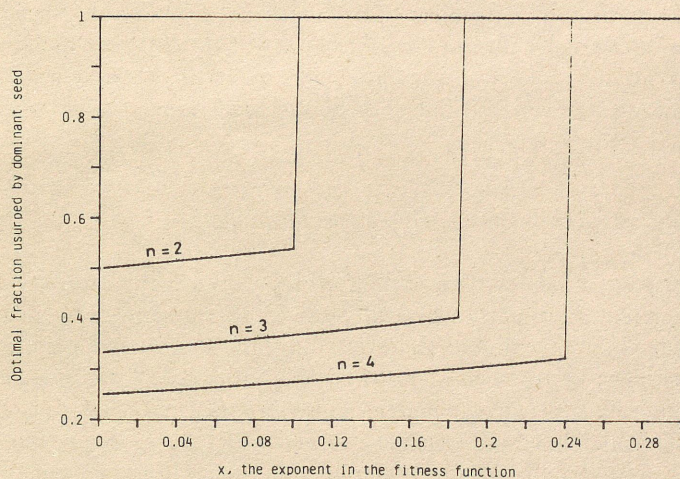


Figure 5. Variation of the optimal fraction ($f = \hat{f}$ or $f = 1$) usurped by the dominant seed at ESS as a function of x for two-seeded, three-seeded, and four-seeded fruits.

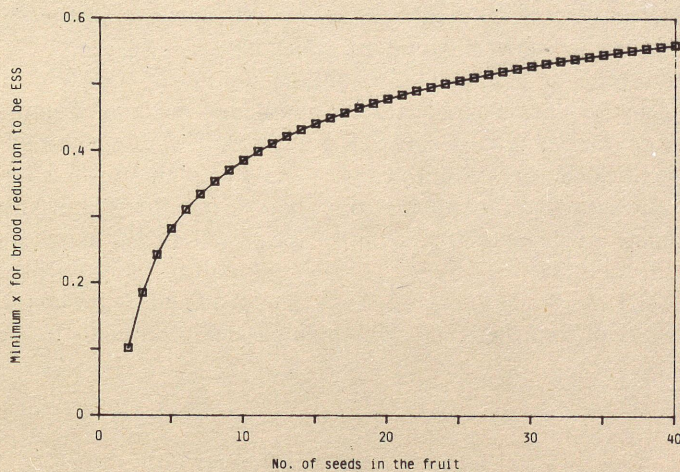


Figure 6. The threshold value of x beyond which brood reduction is the ESS is shown as a function of n , the number of seeds in a fruit.

For a fruit with n seeds, the uninvadable strategy (ESS) corresponds to the resource allocation which maximizes $b - (n-1)c/4$. The optimal allocation in the selfish seed in this situation is seen to be (see appendix, A3)

$$\hat{f} = \frac{1}{n} + \frac{(n-1)x(1 - 4^{1/(x-1)})}{n(1 + (n-1)4^{1/(x-1)})}$$

The variation of \hat{f} with x for different values of n is shown in figure 5 for $n = 2, 3$ and 4. The optimal fraction acquired by the dominant seed for a given value of x is seen to decrease as the number of seeds in a fruit increases, suggesting that the intensity of the conflict among seeds decreases as the number of seeds in a fruit increases.

The minimum value of x necessary for brood reduction to be the ESS is shown in figure 6 as a function of n , the number of seeds in a fruit. The threshold corresponding to a two-seed situation is the lowest, and increases with increasing n . This further emphasizes the decrease in the intensity of the seed-seed conflict with increasing number of seeds in a fruit.

3.3 Predictions of the model and supportive data

The above analysis indicates that sibling rivalry would lead to brood reduction in two-seeded fruits for a broad range of values of x , the exponent in the fitness function (i.e. the efficiency of conversion of resources into fitness). On the one hand, there can be no sibling rivalry in one-seeded fruits. On the other hand, the intensity of sibling rivalry is seen to decrease with an increase in the brood size. In fact, since the inclusive fitness for a selfish allele in an n -seeded fruit is $b - (n - 1)c/4$, the weightage given to the cost increases rapidly with n , thereby decreasing the propensity for brood reduction. Taken together, these results indicate that sibling rivalry would be most intense in two-seeded fruits. Since under such a scenario, loss of one seed is virtually certain, it would not be in the interest of the parent to produce two-ovuled flowers; either only one or very many would be favourable. The model thus predicts that species with two-ovuled flowers would be rather rare.

An examination of the frequency distribution of ovules per flower and seeds per fruit (table 1; Hegde, Uma Shaanker and Ganeshaiyah, personal communication) in over 800 species does reveal the predicted pattern. The frequency of two-ovuled flowers (and two-seeded fruits) is indeed lower than that of one-ovuled or many-ovuled flowers (and one-seeded or many-seeded fruits). Given the complexity of myriad factors that affect ovule and seed number (dispersal mode, habit, packing cost, parent-offspring conflict, etc.: Wiens 1984; Nakamura 1986; Wiens *et al.* 1987; Ganeshaiyah and Uma Shaanker 1988; Uma Shaanker and Ganeshaiyah 1988; Uma Shaanker *et al.* 1990), and the severe simplifying assumption made in the model, the

Table 1. Frequency distribution of ovules per flower and seeds per fruit*.

Size class	Number of species with corresponding number of ovules per flower		Number of species with corresponding number of seeds per fruit	
1	60	(7.43)	177	(21.96)
1-2	147	(18.22)	163	(20.22)
2	64	(7.93)	5	(0.62)
3-5	147	(18.22)	93	(11.54)
> 5	389	(48.20)	368	(45.66)

Numbers in parentheses are percentages.

*Data kindly supplied by Drs S. G. Hegde, R. Uma Shaanker and K. N. Ganeshaiyah.

agreement with the data cannot be said to really validate the model, though it is gratifyingly supportive of it.

3.4 Concluding remarks

One of the consequences of brood reduction is the loss of fitness for the parent. The parent–offspring conflict in such a situation is not over the total quantum of investment (since it is assumed to be constant) but over its differential allocation between sibs. A possible counter-strategy of the parent against brood reduction is polyembryony (Ganeshaiyah *et al.* 1991), whereby the parent produces an extra asexual embryo within the seed. While Ganeshaiyah *et al.* (1991) provided arguments as well as some data in support of this assertion, an explicit population genetic model to demonstrate the same was lacking. These investigations are in progress.

The interplay between parent–offspring conflict and sibling rivalry within a fruit is particularly intricate because of the complex genetic structure (Law and Cannings 1984) of the tissues involved, as perceptively pointed out by Haig and Westoby (1988). The situation could become more interesting if the phenomenon of genomic imprinting (Haig and Westoby 1991) also has a role to play in this conflict. Rather careful genetic modelling may be needed to unravel the relative importance of these possible factors.

Remarkably, however, despite the numerous simplifications, the family level selection models pioneered by Haldane continue to be useful in providing insights into the evolutionary forces governing the patterns of brood size in plants.

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Mathematical appendix

Using the same approach as described in section 2, the conditions on the relative values of benefit and cost for the spread of a selfish allele, for the ESS, and for the threshold for brood reduction are derived here for the general case of n seeds per fruit. As before, it is assumed that in a fruit containing one or more selfish seeds, one of the selfish seeds will acquire a bigger share, and will have a fitness of $1 + b$, while each of the rest of $n - 1$ seeds have an equal share of the remaining resource, and

each a fitness $1 - c$. Alternative ways of sharing resource may easily be imagined; these would form the subject of a separate investigation.

A1. Spread of the selfish allele

Let y (≈ 0) be the frequency of the NS heterozygote, which implies the frequency of pollen to be $y/2$. As before, analysis is carried out to first order only.

Contributions to the frequency of S in the next generation via pollen will be through the fertilization of (N, N, ..., N) flowers by a single S pollen (and $n - 1$ pollen of type N). The frequency of such flowers will be

$$(y/2)n(1 - y) = ny/2, \quad (\text{i})$$

and the fitness of the single NS seed is $1 + b$.

The contributions via ovules will be through the n kinds of flowers, containing $1, 2, \dots, n$ ovules of haplotype S. Since all these will be fertilized by N-type pollen, there would be n kinds of fruits, containing $1, 2, \dots, n$ seeds with genotype NS. The frequency $p(k)$ of fruits with k seeds with genotype NS is given, from binomial distribution, by

$$p(k) = \binom{n}{k} \left(\frac{1}{2}\right)^n y. \quad (\text{ii})$$

The fitness of an NS seed in such a fruit is given by

$$f(k) = 1 + b/k - c(1 - 1/k). \quad (\text{iii})$$

Hence the frequency of the NS genotype in the next generation is given by

$$\begin{aligned} y' &= y \left[\frac{n}{2}(1 + b) + \sum_{k=1}^n p(k) f(k) k \right] / n \\ &= y \left[\frac{n}{2}(1 + b) + \frac{1}{2^n} \sum_{k=1}^n \frac{n!}{k!(n-k)!} (k + b - c(k-1)) \right] / n \\ &= y \left[\frac{n}{2}(1 + b) + \frac{(b+c)}{2^n} \sum_{k=1}^n \frac{n!}{k!(n-k)!} + \frac{(1-c)}{2^n} \sum_{k=1}^n \frac{n!}{k!(n-k)!} k \right] / n. \quad (\text{iv}) \end{aligned}$$

The first summation equals $2^n - 1$, while the second equals $n(2^{n-1})$. Substituting and simplifying,

$$y' = y \left[n + (b+c) \left(1 - \frac{1}{2^n}\right) + (b-c) \frac{n}{2} \right] / n,$$

and thus y' will be greater than y if

$$(b+c) \left(1 - \frac{1}{2^n}\right) + (b-c) \frac{n}{2} > 0.$$

Further simplification shows the condition for the spread of the selfish allele to be

$$b > c \left(\frac{2^{n-1}(n-2) + 1}{2^{n-1}(n+2) - 1} \right).$$

A2. *Evolutionarily stable strategy*

As in section 2, let z (≈ 0) be the frequency of SS' genotypes, which implies the frequency of S' pollen to be $z/2$.

Arguing along the lines similar to the ones in section A1, the contributions to the next generation of S' via pollen will come from fruits with one SS' seed (and $n-1$ seeds of SS genotype), whose fitness would be $1 + b'/n - c(1 - 1/n)$.

This is because, the probability that the SS' seed will be the "winner" is $1/n$, and the corresponding fitness is $1 + b'$. The probability that the winner is SS is $(n-1)/n$, and the fitness to SS' in such a situation is $1 - c$.

For the contribution to the next generation via ovules, the frequency of flowers containing k pollens of type S' is given by equation (ii) (except for z in place of y). However, the fitness of an SS' seed from such a fruit is

$$f(k) = 1 + \frac{b'}{n} - c' \left(\frac{k-1}{n} \right) - c \left(\frac{n-k}{n} \right).$$

The net fitness of the SS' genotype is given by

$$\begin{aligned} & \left[n \frac{z}{2} \left\{ 1 + \frac{b'}{n} - c \left(1 - \frac{1}{n} \right) \right\} + z \sum_{k=1}^n p(k) f(k) k \right] / z \\ & = n + b' - \frac{3}{4}(n-1)c - \frac{(n-1)c'}{4}. \end{aligned}$$

This has to be greater than the fitness of the SS genotype which is $n + b - (n-1)c$. Hence, fitness of SS' > fitness of SS if

$$b' - (n-1)c'/4 > b - (n-1)c/4.$$

Thus, the strategy which maximizes $b - (n-1)c/4$ would be able to invade any other strategy, and will be uninvadable by any other strategy, and hence will be the ESS.

A3. *Threshold for brood reduction*

The net resource invested by the parent in the fruit with n seeds is (section 2.4) equal to $n/(1-x)$. If the dominant seed usurps a fraction $f > 1/n$, its fitness is

$$F' = \left(\frac{fn}{1-x} - 1 \right)^x,$$

and the fitness of each of the rest of the seeds is

$$F'' = \left(\frac{(1-f)n}{(n-1)(1-x)} - 1 \right)^x.$$

These can be used to derive \hat{f} , the optimal allocation, in the same manner as in

section 2.4, the expression for \hat{f} being

$$\hat{f} = \frac{1}{n} + \frac{(n-1)x(1-4^{1/(x-1)})}{n(1+(n-1)4^{1/(x-1)})}$$

Let b and c be the corresponding benefits and costs.

As long as $f < (n-1)/n$, each of the seeds other than the dominant obtains at least one unit of resource, and is thus viable. For $f > (n-1)/n$, only one seed survives, and brood reduction takes place.

When the entire resource is usurped by the dominant seed ($f = 1$), its fitness is

$$F^* = \left(\frac{n}{1-x} - 1 \right)^x$$

Let b^* be the benefit, while the cost c is unity.

If $b^* - (n-1)/4$ is greater than $b - (n-1)c/4$, then $f = 1$ is the ESS, and brood reduction takes place; only the dominant seed survives and the rest are aborted.

These criteria may be used to obtain the threshold value of x for brood reduction to occur in n -seeded fruits.

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