

palate of M16649 and the much greater height of the buccal cusp and the greater cingulum development in M35145. In all these characters the specimens from Saudi Arabia retain, with *Proconsul* species, what is interpreted as the primitive condition for the Hominoidea<sup>6</sup>. They lack the synapomorphies of the *Ramapithecus*–*Sivapithecus* lineage of Asia<sup>6–8</sup>, and thus cannot be grouped taxonomically with these genera, but as they share only primitive characters with *Proconsul*, they cannot, on present evidence, be grouped with that genus either. The conformation of the mandible, when it is known, should show whether these specimens belong to the genus *Proconsul*, and until we have additional evidence we have decided not to name these specimens.

The known range of dryopithecines in Africa during the Miocene has been greatly increased by these discoveries in Saudi Arabia. This area must have been close to the migration routes between Africa and Eurasia, and it is therefore of great significance that there is no evidence linking these specimens with the contemporary species of *Sivapithecus* from Turkey<sup>9</sup>. The Turkish deposits at Pasalar are similar in age to the Saudi Arabian deposits, but their *Sivapithecus* species shares synapomorphies with later Miocene species of the genus from India and Pakistan<sup>8</sup> that are not present in the Saudi Arabian specimens. This could indicate that the new specimens from Saudi Arabia represent a primitive branch of the Dryopithecinae that was not directly related to any of the later pongid lineages.

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## Stability and diversity of ecological communities

MAY<sup>1</sup> drew an analogy between large randomly connected cybernetic networks<sup>2,3</sup> and ecosystems. His analysis of stability criteria for such networks seems to contradict the traditional ecological hypothesis that ecosystem diversity contributes to functional stability<sup>4–7</sup>. May's analytical solution for large matrices in which each element by itself is stable showed that<sup>1</sup> "too rich a web connectance or too large an average interaction strength leads to instability. The larger the number of species, the more pronounced the effect". As the number of elements in the matrix increases, the transition region between stability and instability becomes increasingly narrow<sup>1–3</sup>. Thus, a complex system perched near this transition region is subject to a self-generating catastrophe upon only a minor modification of system parameters. If these models are applicable to real ecosystems, they obviously have immense implications for resource management as well as ecological theory. I report here an application of May's conclusion to a real ecological system.

These cybernetic systems have three parameters<sup>1–3</sup>: (1) the number of elements,  $n$ , in the interaction matrix. (2) An average interaction term,  $i$ , which characterises the average effect of each element on each other element; overall,  $i$  is

bounded at +1 and -1. (3) A connectance,  $c$ , which is the proportion of non-zero  $i$ 's in the matrix. Each element in the matrix, in isolation, will return to its equilibrium value if perturbed because of negative self-damping terms; the rate of return will be determined by the magnitude of the self-damping term. Stability is defined by a matrix in which all real parts of latent roots are negative<sup>1,3</sup>. May<sup>1</sup> showed that very large systems are almost certainly stable if

$$i < (nc)^{-1/2} \quad (1)$$

and unstable if

$$i > (nc)^{-1/2} \quad (2)$$

Even for relatively small matrices, the analytical solution agrees well with Monte Carlo simulations<sup>1,8</sup>. If equation (1) holds, any matrix element perturbed from its equilibrium will return there.

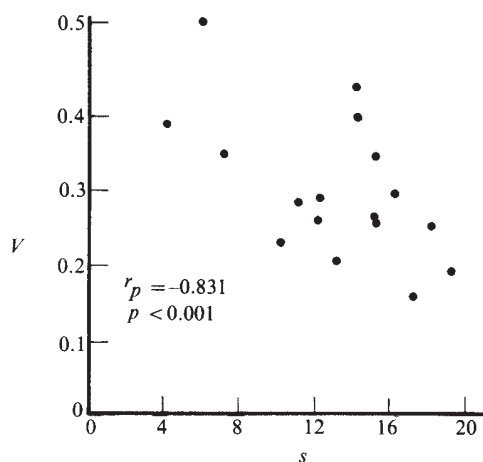
Although May's conclusion is widely cited as evidence contradicting the conventional ecological wisdom that ecosystem functional stability is facilitated by diversity, I know of no application of it to real ecological systems. I report here such an application giving evidence that more diverse plant communities are likely to be more stable, by May's criterion, than less diverse plant communities. Because these models lack much of the intrinsic structure of trophic webs<sup>9,10</sup> it seems most appropriate to apply them to a single trophic level, as I do here.

A common problem in applying mathematical models to ecological systems is measuring parameters in ecological terms that are compatible with specifications of the model. I propose the following approaches to measuring  $n$ ,  $i$ , and  $c$  in nature: Following May's analogy, I call the number of species,  $s$ , the number of interaction elements. I measure interaction among species by applying the point correlation coefficient<sup>11</sup>,  $V$ , to nearest neighbour data<sup>12</sup>.  $V$  has the same limits as  $i$ , being +1 if two species always occur together, and -1 if they never occur as adjacent individuals. There is ample evidence suggesting that local positive associations are caused by facilitation<sup>13,14</sup> and negative associations by competition and resultant habitat segregation<sup>13–15</sup>. I estimate the average interaction term,  $i$ , as the mean value of significant  $V$ 's ( $P < 0.05$  for  $V = 0$ ). As negative associations are much more common than positive associations in the grasslands studied, I changed the sign of mean  $V$  to positive for convenience. Following rules of the cybernetic matrices<sup>1,3</sup>, I define  $c$  as the proportion of all  $V$ 's that were significantly different from zero.

Data were collected in 17 grassland stands in Tanzania's Serengeti National Park during May and June 1977, a period of peak above-ground plant biomass. Species identities of the individual nearest to a random sampling point, and of its nearest neighbour, were recorded for 100 sampling points in each stand. If the primary and secondary individuals were the same species, the closest individual of another species was recorded. The range of vegetation sampled was designed to be representative of the range of grassland communities identified by clustering data from 105 stands<sup>16</sup>.  $V$  was calculated only when each species was represented by at least 10 individuals. As points rather than species were the random sampling criterion, data were corrected for sample size. That is, the number of possible associations increases as  $(s^2 - s)/2$  so the probability of recording 10 individuals of all species for a standard sample size decreases with  $s$ . This was corrected for by applying the partial correlation coefficient,  $r_p$ , holding  $V_c/V_p$  constant, where  $V_c$  was the number of associations calculated based on the limit at 10 individuals and  $V_p$  was  $(s^2 - s)/2$ .

Inspection of equations (1) and (2) shows that stability might increase with diversity if interaction strength and connectance declined as more species were added<sup>1</sup>. I found that both average interaction strength (Fig. 1) and connectance (Fig. 2) declined as species richness of the grassland increased. The correlation was somewhat stronger for interaction strength than for connectance.

These data provide empirical support for two conjectures about how natural communities are organised, and how this

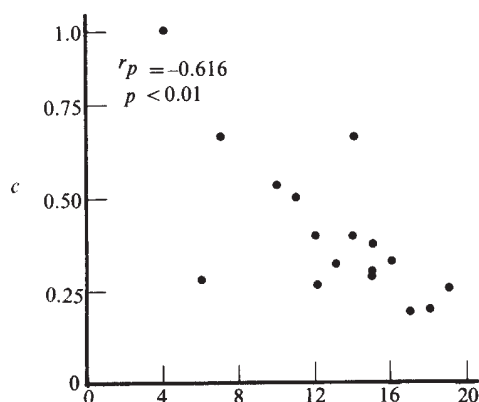


**Fig. 1** relationship between average interaction strength among species and number of species in African grassland samples.  $r_p$  is the partial correlation coefficient with sample size held constant.

organisation may affect relationships between community diversity and stability. First, species-poor communities are likely to be characterised by strong interactions among the species while species interacting with many others are likely to do so weakly<sup>17</sup>. Thus, diffuse competition<sup>18</sup> becomes more important as species diversity increases. Second, it suggests that communities are organised as blocks of species which interact among themselves but interact little with species in other blocks. May<sup>1</sup> remarked that such an organisation might reduce the destabilising effect of greater system complexity. I suggest that such interacting blocks of species represent guilds<sup>19</sup> of species segregating along similar resources, and that they are only weakly connected with other guilds segregating along other gradients. Guild size may be estimated from  $sc$ . I found this product remarkably uniform for the 17 grasslands sampled:  $sc = 4.7 \pm 0.7$  (0.95 interval) species per guild. For the Serengeti grassland, then, a guild may consist of remarkably uniform blocks of four to five species. Speculation about the environmental gradients organising such guilds in plant communities seems injudicious at this time. Numerous alternatives are possible.

The ratio,  $i/(sc)^{-1/2}$ , may be used as an instability index; if it is greater than 1, the system has a zero probability of being stable; if it is less than 1, it will be stable. Since both interaction strength and connectance declined with species richness, and  $sc \approx$  constant in these samples, it is obvious that the ratio also must decrease. There was a significant negative correlation

**Fig. 2** Relationship between connectance and number of species in African grassland samples.



between the index and  $s$  ( $r_p = -0.594$  for  $P < 0.02$  with  $df = 14$ ). Mean value of the ratio was  $0.65 \pm 0.12$  (0.95 interval). Only one stand, with a ratio of 1.39, fell above the critical limit of 1. In general, these grasslands would be expected to return to their equilibrium relative abundance relations if perturbed. They are stable by May's criterion<sup>1</sup>.

Fragmentary evidence is available indicating that relative abundance relations are more stable, with environmental changes, as  $i/(sc)^{-1/2}$  decreases. I reexamined in 1975 a series of four exclosures built in the early 1960s<sup>20</sup>, evaluating the stability of relative abundances by the coefficient of similarity<sup>21</sup> between protected and unprotected vegetation. The closer the similarity was to 1, the less species composition had changed subsequent to protection from grazing. As the ratio of interaction strength to the richness-connectance function increased in the unprotected vegetation, the less similar were species abundance relations in protected and unprotected vegetation (Table 1). Sample size is so small that statistical comparison seems inadvisable, but these data suggest a greater tendency for vegetation with weak interactions and low connectance to maintain species abundance relations when the environment changes.

In conclusion, I believe May's arguments do not contradict the traditional ecological hypothesis that ecosystem stability increases with ecosystem diversity. Rather, these arguments provide considerable fresh insight into the organisational constraints within ecosystems that may contribute to an association between diversity and stability. The occurrence of species as guilds with a relatively low number of participants, which interact weakly if at all with other guilds, may be an important component of ecosystem organisation. This is a consequence of

**Table 1** Similarity of species relative abundance relations in unprotected grasslands and areas protected from grazing for over 10 yr and the instability index for unprotected areas

Similarity (C)	Instability ( $i/(sc)^{-1/2}$ )
0.022	0.571
0.365	0.537
0.419	0.433
0.539	0.348

a decline in connectance as diversity increases. If connectance were constant, the number of species per guild would be a linear function of the total number of species with slope = connectance. Even among those species which interact, the average strength of interaction may decline as diversity increases. Thus, more diverse ecosystems may be more stable than less diverse systems because (1) connectance declines as diversity increases, (2) species are therefore organised as relatively small guilds, and (3) interaction strength among species declines as diversity increases.

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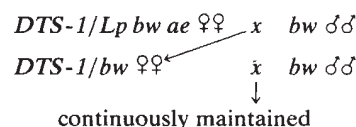
## Genetic sexing technique for a mosquito sterile male release

DURING the course of an experiment to assess the efficiency of a breeding system to detect visible and lethal mutants on chromosome 3, a dominant, temperature-sensitive lethal (DTS) was discovered in the mosquito, *Culex tritaeniorhynchus* Giles, an important arbovirus vector. This DTS lethal, designated  $L(3)I^{DTS}$  but here referred to as *DTS-1*, survives at 26°C but dies at 32°C during the larval stages. It was recovered after treatment with 0.005 M ethyl methanesulphonate (EMS). The isolation of a sex-linked DTS in a vector species of medical or agricultural importance may be valuable as a sexing device in a release programme involving either males sterilised directly by radiation or chemosterilants or males carrying genetic aberrations that give high semisterility.

The use of conditional lethals such as temperature sensitivity in insect control has been suggested by several investigators<sup>1–7</sup>. While conditional lethals, especially temperature-sensitive ones, may be potentially useful in limiting natural populations, they can also be used as a sexing device in a sterile male release programme. The sexing of insects for release may be difficult, expensive and time consuming if it involves laborious sorting by hand, or less than 100% efficient by the use of mechanical devices. A genetic sexing method would also save space and labour as only those individuals for release are reared. In two species of medical importance, houseflies, *Musca domestica* L.<sup>8</sup> and mosquitoes, *Cx tritaeniorhynchus* Giles<sup>9</sup> recessive heat-sensitive lethal mutations have been isolated, after treatment with EMS, that can be used in combination with the sex-determining factors as a method of sexing adults for a sterile male release programme. However, the possibility of incorporating the genome from a wild population into the genotype of males to be released renders a dominant temperature-sensitive lethal superior to a recessive one in a scheme to produce progeny of only one sex. Recently for the mosquito, *Anopheles gambiae* Giles, a genetic sexing mechanism was produced which involved the use of a conditional lethal, diel-drin resistance, and a translocation<sup>10</sup>. Using this method, diel-drin-resistant sterile or semisterile males would be released into the field. The authors of the method suggest that this could be considered, as diel-drin resistance is already common in insect pest populations and this insecticide and its analogues are unlikely to be used as control agents because of this and because of their toxicity hazards.

In *Cx tritaeniorhynchus* ( $2n = 6$ ) genetic systems are available to detect lethal and visible mutations on chromosomes 1<sup>9,11</sup> and 2<sup>12</sup>. A pericentric inversion,  $In(3)I$ , had been isolated that reduced recombination in males carrying the  $M^3$  sex allele<sup>13,14</sup> between the two linkage group III terminal markers long palpi<sup>15</sup>, *Lp*, and abnormal eye<sup>16</sup>, *ae*, from 50 map units to approximately 10 map units. Incorporating this crossover suppressor and *Lp*,  $M^3$ , *ae*, and *bw*<sup>16</sup> (brown eye, a recessive about 15 map units from *ae*) a mating scheme has been devised

in which a major portion of linkage group III is rendered homozygous to detect lethal and visible mutations (Fig. 1). In an experiment to assess the efficacy of this scheme an isogenic stock had been isolated which seemed to be free of recessive lethals at 26° and 32 °C. At both temperatures most of the first instar larvae usually develop into adults. Males from this stock were then treated with 0.005 M EMS to isolate visible mutants and temperature-sensitive lethals on chromosome 3. However, the control (males not treated with EMS) gave erratic results which suggested that either the original isogenic stock was no longer lethal-free or that recessive lethals had been introduced from the tester males. The latter was possible as  $In(3)I$  allowed at least 10% crossing over between *Lp* and *ae*. Therefore, the entire experiment was discarded except for one line (out of the 169 investigated) which indicated the possible presence of a DTS lethal. In this line only 5 *bw* ♂♂ were found in the  $F_3$  family reared at 32 °C while 11 *Lp* ♀♀, 16+♂♂ and 9 *bw* ♂♂ were recovered from the family reared at 26 °C. In the  $F_4$  generation similar results were obtained at 32 °C in which the one family tested had only 18 *bw* ♂♂ while at 26 °C there were 19 *Lp* ♀♀, 16+♂♂ and 18 *bw* ♂♂. The lack of +♀♀ suggested that the *DTS-1* homozygote was itself lethal or that other recessive lethals had been induced elsewhere on the chromosome. The  $F_4$  generation *Lp* ♀♀ carrying the *DTS-1* chromosome were then outcrossed to males from the *bw* laboratory strain for two successive generations at 26 °C:



In this maintenance breeding system all individuals with normal eyes carry the *DTS-1* mutant, which can be distinguished from the homozygous *bw* at all life stages (embryos, larvae, pupae and adults) and at all temperatures, and can be checked every generation for contamination or modification by rearing some families or part of individual families at 32 °C and 26 °C.

Using this mating scheme, we reared larvae at 26°, 28°, 30° and 32 °C to determine more precisely the lethal temperature. The results (Table 1) indicate a reduction in survival of the *DTS-1* from 26° to 32 °C with the lethal temperature between 30° and 32 °C. At 26 °C the *DTS-1* chromosome actually exhibited greater survival than the *bw*-carrying chromosome. Daily examination of the cultures reared at 32 °C indicated that the lethal phase, the development stage at which death occurs, is usually in the second and sometimes in the third instar. At 32 °C the *DTS-1* individuals remained as second instars for 2–3 d without moulting and then died while the *bw* larvae continued development with only 1 d spent at the second instar stage. By the time the *bw* larvae were in the fourth instar, most of the *DTS-1* larvae were dead.

The temperature-sensitive period, the developmental interval in which the mutant was irrevocably committed to death by the restrictive temperature, was determined tentatively by a preliminary series of reciprocal shift-up, shift-down and double

**Table 1** Results of crosses *DTS-1/bw* ♀ × *bw* ♂ reared at 26 °C, 28 °C, 30 °C and 32 °C

Temperature (°C)	No. larvae/adults		% Survival larvae to adults		Survival ratio <i>DTS-1/bw</i>
	<i>DTS-1</i>	<i>bw</i>	<i>DTS-1</i>	<i>bw</i>	
26	173/133	147/94	76.9	63.9	1.20
28	157/105	151/112	66.9	74.2	0.90
30	204/27	202/125	13.2	61.9	0.21
32	275/0	294/213	0	72.4	0