Pirineos, **138**: 3 a 28, JACA; 1991

THE USE OF ECOLOGICAL THEORY AND AUTECOLOGICAL DATASETS IN STUDIES OF ENDANGERED PLANT AND ANIMAL SPECIES AND COMMUNITIES[1]

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SUMMARY.- Few, if any, European habitats have been unaffected by modern land-use and the problems of conserving the diversity of the European flora and fauna are both urgent and immense. This paper describes a simple method for analyzing floristic change that is hoped will prove useful for assessing the nature and severity of these threats. The method involves the use of ecological theory and the collection of simple autecological data. Examples are given to illustrate how this approach can be used both to identify reasons for floristic change and to provide functional analyses of phytosociological data. Also, as a result of analyses of reasons for commonness and rarity in butterflies and birds, it is argued that similar functional interpretations of zoological datasets may soon be possible.

RESUMEN.- Considerando que prácticamente todos los hábitats de Europa han sido afectados por los usos de la tierra modernos, la conservación de la diversidad de su flora y fauna se presenta como un problema muy grave y urgente. En este articulo se describe un método simple para analizar cambios florísticos, contemplando el uso de la teoría ecológica y la colección de datos autoecológicos sencillos. Dicho método constituye una herramienta para evaluar la naturaleza y severidad de procesos de pérdida de la diversidad biológica. Se dan ejemplos ilustrando el uso de este enfoque en la identificación de las causas de cambios florísticos y en el análisis funcional de datos fitosociológicos. Se presentan, además, las razones que explican la presencia de especies raras o muy comunes de mariposas y aves. A partir de estos últimos resultados, se concluye que en breve será posible realizar una interpretación funcional similar de datos zoológicos.

ZUSAMMENFASSUNG.- Nur wenige, wenn überhaupt, der Lebensräme in Europa sind unberührt von moderner Landnutzung und die Probleme der Erhaltung der Vielfalt in der Flora und Fauna sind sowohl dringend als auch immens. Dieser Artikel beschreibt eine einfache Methode um die Veränderungen in der floristischen Zusammensetzung zu untersuchen. Diese Methode wird sich hoffentlich als nützlich für die Abschätzung von Ausprägung und Intensität dieser Bedrohungen herausstellen. Die Methode beinhaltet die Benutzung von ökologischer Theory und die Samlung einfacher

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[1] Received, November 1991.

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autökologischer Daten. Es werden Beispiele gegeben, die illustrieren sollen, wie diese Vorgehensweise benutzt werden kann, um zum einen die Gründe für den Wandel in der floristischen Zusammensetzung zu identifiziern und zum anderen eine funktionale Analyse pflanzensoziologischer Daten bereitzustellen. Außerdem wird dargestellt, daß als ein Ergebnis einer Untersuchung der Gründe für die Häufigkeit und Seltenheit von Vögeln und Schmetterlingen eine ähnlich funktional begründete Interpretation zoologischer Daten sehr bald möglich sein wird.

Key words: interpreting floristic change, interpreting faunistic change, land-use, conservation.

The vegetation of Spain, like that of the United Kingdom and Europe in general, is changing. Modern practices of land use are leading to the modification or destruction of climax vegetation and of many of the habitats created through traditional agriculture (see LASANTA-MARTINEZ 1988, 1990). Superimposed upon this is the additional threat of climate warming.

Since so many Spanish ecosystems are threatened, the detailed ecological study of each prior to any implemention of conservation measures is impractical. It is, therefore, desirable to supplement the relatively few ongoing intensive studies of ecosystems with simpler, less time-consuming and inevitably less exact functional analyses. This paper will outline one such procedure, the Functional Interpretation of Botanical Surveys, known by the acronym FIBS and devoloped at the NERC Unit of Comparative Plant Ecology. The theoretical background to FIBS and examples of its potential to interpret the reasons for floristic change will be illustrated. However, conservation of plants should not be considered in isolation from conservation of animals, and this paper will also examine the life-history characteristics of common and of rare (potentially threatened) animal species. It will be argued that land-use affects the distribution and abundance of both animals and plants in remarkably similar ways. This holds out the prospect that methods similar to those used for plants can be developed for interpreting both the functional characteristics of faunas and faunistic change.

1. Functional analyses of floristic datasets by FIBS

1.1. *Theoretical Background*

1.1.1. Plant Strategy Theory (sensu GRIME, 1979): According to GRIME (1979) two factors limit the accumulation of biomass of the established phase of the plant. One factor is 'stress', which constrains the rate and extent of growth. The other is 'disturbance', which results directly in the destruction of biomass.

Stressed habitats, (e.g. bare rock surfaces and unproductive calcareous pasture) are exploited mainly by 'stress-tolerators'. These are slow-growing, long-lived, evergreen species which are able to survive for long periods under conditions unfavourable for growth but which are also relatively unresponsive to any amelioration of the environment. They are, because of their slow growth-rate, sensitive to both disturbance (regrowth of destroyed tissue is slow) and eutrophication (stress tolerator are at a competitive disadvantage to other, faster-growing species). Typical stress-tolerators are lichens and *Festuca ovina.*

Fertile but disturbed habitats (e.g. arable land) are characteristically the home of ruderals. Ruderals grow rapidly but are short-lived, producing flowers and setting seed at an early stage of growth. Typical ruderals include *Euphorbia peplus, Poa annua* and *Setaria viridis.*

Where the effects of stress and disturbance are minimal (i.e. where conditions for plant growth are close to optimal) a third group of species, 'competitors', prevail. These are fast-growing species which tend to monopolise available resources leading to the competitive exclusion of most other potential component of the vegetation. *Arundo donax, Epilobium hirsutum, Phragmites australis* and *Urtica dioica* are all typical competitors.

Grime's theory also predicts that no species can exploit sites which combine high stress with high disturbance. Thus the tree primary strategies recognised; stress-tolerant, ruderal and competitive along with four intermediate strategies can be positioned within and equilateral triangle as illustrated in Fig. 1a. Species can be ascribed to thir established strategy using the dichotomous key presented in GRIME (1986).

The proportion of species with different strategies is likely to change within vegetation in response to changing land use. For example, in the event of eutrophication, species which grow more rapidly will tend to increase. In the case of vegetation where CSR strategists prevail this will result in an increase in competitors (abbreviated as C), ruderals (R) and the intermediate strategy, competitive ruderal (CR)-as is illustrated in Fig. 1b. The theoretically-expected effect of various other management scenarios are presented in Fig. 1c-f.

1.1.2. Other attributes. It must be emphasised that strategy theory, described more fully in GRIME (1979), is, as its name indicates, simply a theory. Althoug it does in practice appear to provide sensible answers to a variety of ecological problems (HODGSON 1989, 1990, 1991), strategy theory must be used with caution, at least until current tests of its validity being carried out at Sheffield are completed. Therefore, it is advisable to consider other additional ecological attributes when analysing floristic datasets.

Some information for relevant ecological attributes is relatively easy to obtain and data for a wide variety of species characteristics have already been collected for 502 of the commoner British species (GRIME, HODGSON & HUNT 1988). With the exception of persistence of seed in the soil, an important but difficult to assess attribute, following are arguably the easiest, and most informative to measure.

I. the commonest habitats in which the species occurs (in Central England wetland, rocky, arable, pasture, spoil, wasteland and woodland are separated-see GRIME *et al,* 1988).

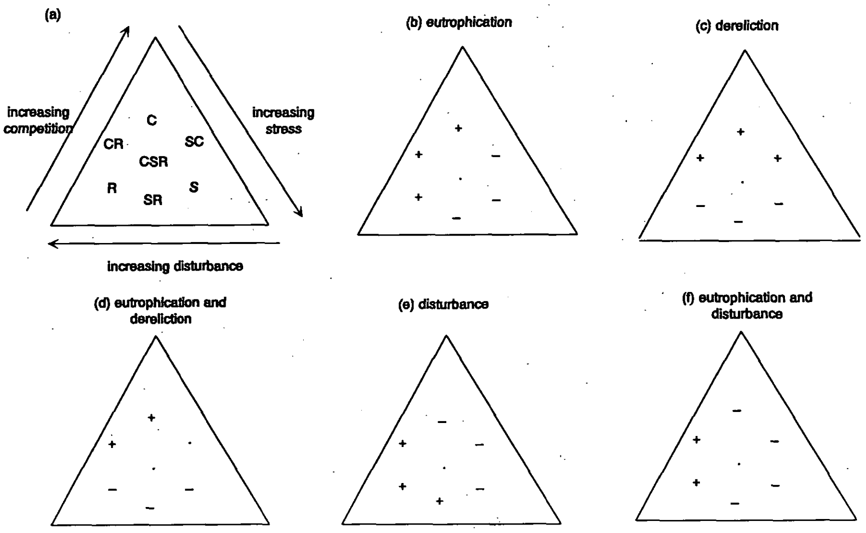


Figure 1: The Plant Strategies of Grime (1974) and their theoretically expected changes in response to various effects of modern land-use. Strategies are abbreviated as follows, C, competitive; S, stress tolerant; R, ruderal; CR, competitive ruderal; SC, stress-tolerant competitive; CSR, CSR-strategist. In b-f favoured strategies are indicated by a '+' and unfavoured strategies by a '-'. Less affected strategies are indicated by a dot. The scenerio illustrated relates to vegetation where a majority of species are CSR-strategists. However, the principles are the same whatever strategy predominates. For example, had most species been stress-tolerators, favoured strategies would also have included under conditions of eutrophication (see triangle b) CSR- strategists.

II. regenerative strategies
particularly (a) the production of a persistent seed bank (e.g. *Anagallis arvensis* and *Ulex* spp).
[This strategy, for dispersal in time, permits species to survive in habitats subject to periods of extreme disturbance (e.g. through ploughing or burning)].
and (b) the production of numerous, wind-dispersed seeds or spores (e.g. *Epilobium* spp, orchids and ferns).
[This strategy, for dispersal in space, allows habitats to be colonized from a distance following disturbance].

III. canopy structure (rosette, semi-rosette, leafy).

IV. maximum height of canopy (8 classes separated in GRIME *et al*, 1988).

V. lateral spread of clonal patches (5 classes as in GRIME *et al*, 1988).

VI. leaf phenology (evergreen or seasonal).

Many of these atributes will be responsive to changes in land management (Table 1) providing valuable additional data for assesing the functional characteristics of vegetation. However, to date, identifying the effects of eutrophication is still primarily dependent upon plant strategy theory.

TABLE 1.

Species attributes theoretically expected to be favoured (+) or disfavoured (-) by disturbance, eutrophication and dereliction. Relationships give in parenthesis will occur less consistently than those not in brackets. Characters unaffected by land-use or where changes will be rather inconsistent and/or slow are indicated by a '.'.

	increased disturbance		*increased eutrophication*	*increased dereliction*
	A. through ploughing, burning etc.	*B. through grazing*		
I. Commonest Habitats				
rocky	(+)	(+)	.	-
arable	+	(+)	.	-
pasture	-	+	.	-
spoil	(+)	.	(+)	.
wasteland	-	-	.	+
woodland	-	-	.	(+)
II. Regenerative Strategy				
persistent seed bank	+	.	.	.
numerous wind-dispersed seeds	+	.	.	.
III. Canopy Structure				
rosette	.	+	.	-
leafy	.	-	.	+
IV. Maximum Height of Canopy				
≤ 300 mm.	.	+	.	-
> 600 mm.	.	-	.	+
V. Lateral Spread				
clonal patch < 250 mm.	+	.	.	-
> 1.000 mm.	(-)	.	.	+

1.2. *Analyses of data from field experiments*

Ploughing followed by fencing to exclude livestock has changed the flora of an experimental plot near Leon, Spain (Table 2) and a FIBS analysis utilizing autecological data collected from the United Kingdom has been used to interpret these changes. The pasture itself is relatively unproductive with

TABLE 2.

The effect of ploughing and excluding grazing on the floristic composition of montane pasture in the Piedrafita Pass, Leon, Spain (data from Hodgson et al (in preparation). These lists were prepared three years after the ploughing + exclusion of grazing treatment had been set up. Species absent from C. England are denoted by an asterisk.

	grazed (control)	ungrazed * ploughed
	(% frequency)	
More or equally frequent in ungrazed + ploughed treatment		
Achillea millefolium	100	100
Cerastium fontanum	50	88
Galium saxatile	0	13
Hieracium gr. pilosella	100	100
Jasione montana	13	13
Rumex acetosella	100	100
Veronica arvensis	50	88
V. officinalis	13	13
V. serpyllifolia	13	63
More frequent in control treatment		
Agrostis capillaris	100	88
Carex caryophyllea	25	0
*Cerastium pumilum	13	0
Dianthus deltoides	13	0
*Euphrasia hirtella	0	13
Festuca nigrescens	100	50
*Herniaria ciliata	13	0
Lotus corniculatus	100	0
Luzula campestris	38	0
Plantago lanceolata	100	75
Ranunculus bulbosus	38	13
*Sagina saginoides	50	0
Sedum anglicum	13	0
Silene nutans	13	0
Thymus praecox	75	25
Trifolium repens	88	63
No of species per quadrat ± standard deviation	11.9±1.6	9.1±2.3
Mean vegetation height (cm.) ±S.D.	1.6±0.3	9.1±3.4
% bare soil ±S.D.	0	60±18
N.º of 0.25 m² quadrats	8	8

CSR strategists predominating and, as expected in an area where fire is an important management tool, most species form a persistent seed bank (Fig. 2).

The two components of the treatment, ploughing and fencing to exclude livestock, are likely to have rather different effects and will, therefore, be considered separately.

a) Disturbance by ploughing should, on theoretical grounds, lead to an increase in the proportion of ruderals (and monocarpic and arable species) and to a decrease in the proportion of stress-tolerators, the species that recover most slowly from damage, and the results in Fig. 2 are entirely consistent with this scenerio. The creation of areas of bare soil will also encourage the seedling establishment of species that produce numerous wind-dispersed seeds and those whose seed persists in the soil and there is, indeed, an increase in species with these regenerative strategies, although in the case of species with a persistent seed bank, the increase is not statistically significant (Fig. 2).

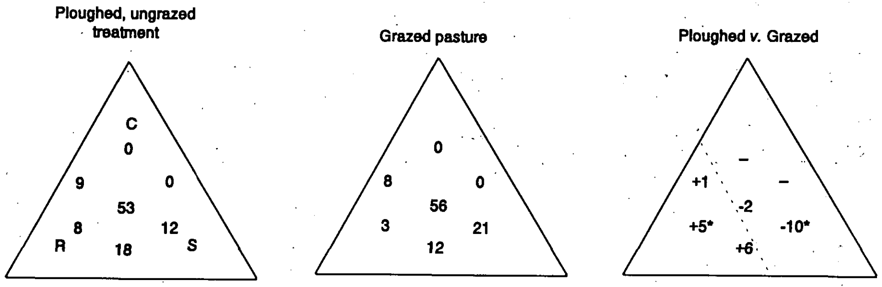


Figure 2: A comparison of the functional characteristics of ploughed, ungrazed and grazed grassland (control treatment) in the Piedrafita Pass, León, Spain -an analysis of the floristic data presented in Table 3. Functional data refer to the ecological characteristics of the species not in Spain but in the United Kingdom and were abstracted from GRIME *et al* (1988) and HODGSON (unpublished data-base).

Habitat type of component species (%)	ploughed and ungrazed	grazed pasture	
Arable	17±4	12±3	z=-2.28*
Pasture	69±7	69±8	z=-0.05 NS
Rocky ground	15±8	16±15	z=-1.20 NS
Wasteland	35±6	43±7	z=-2.01*
Monocarpic species (%)	19±3	10±8	z=-2.44*
Canopy height ≤ 300 mm.	100	100	
Widely-dispersed seeds (%)	12±4	9±2	z=-2.10*
Persistent seed bank (%)	95±6	90±2	z=-1.18 NS
% decreasing	35±10	51±7	z=-2.81**
% increasing	43±9	31±7	z=-2.32*
associated with species-rich vegetation (spp >22 m^{-2})	5±6	12±8	z=-1.28 NS
no of samples	8	8	

b) Excluding grazing stock is a form of dereliction that in the short term may be expected to increase the percentage of species with more competitive strategies *sensu* GRIME (1979), species with a tall canopy and those from wasteland, an unmanaged habitat. However, there is no evidence in Fig. 2 of such changes; indeed the control treatment, grazed pasture, has a greater proportion of species characteristic of wasteland. This may be due to an unplanned continuation of disturbance caused by the activities of *Microtus arvalis,* which has preferentially colonized the stock-proof exclosure.

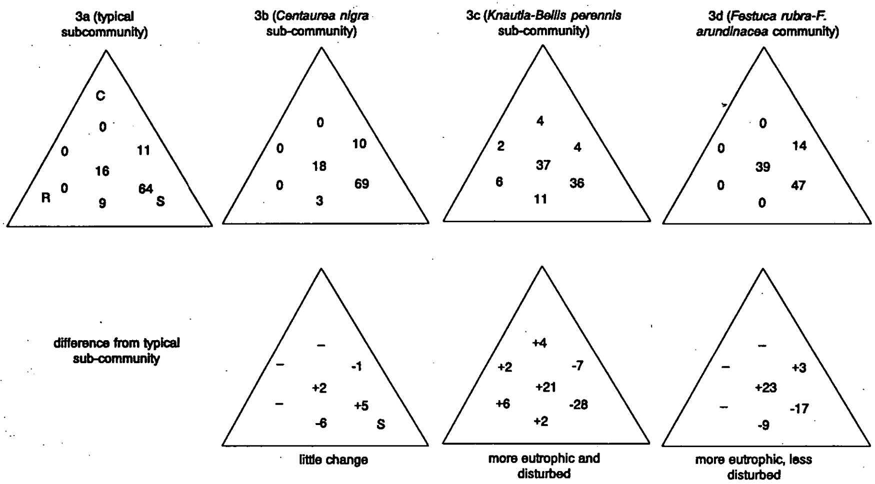
Thus, in this rather simple example of a FIBS analysis disturbance, initially through ploughing and subsequently through the burrowing activities of *Microtus arvalis,* appears to have been the main reason for vegetational change. Any effect of excluding grazing animals in the three years since the experiment was set up has been minor and removal of grazing may paradoxically have enhanced the effects of disturbance by increasing seed-set (preventing inflorescences from being consumed). Additional analyses of the 'ungrazed and unploughed' and 'grazed and ploughed' treatments also present in the experiment will help to elucidate the relative effects of grazing, abandonment, ploughing and *Microtus arvalis.*

1.3. *Analyses of phytosociological data*

Many extensive phytosociological studies have been carried out in Europe and, for example, the major vegetation types within much of Spain have been described (BRAUN-BLANQUET & BOLOS, 1957; BOLOS, 1967; RIVAS MARTINEZ *et al.,* 1984; PIENADO LORCA & RIVAS MARTINEZ, 1987). Phytosociological surveys of this type can provide a potentially rich source of data for analysis by FIBS as will be illustrated using data from a major phytosociological study of British vegetation recently completed for the Nature Conservancy Council (see RODWELL, 1991).

1.3.1. Identifying the principle ecological characteristics of plant communities. This first FIBS analysis considers *Bromus erectus* and related types of calcareous grassland. It assumes that the principle functional characteristics of each sub-community can be identified by analyses of lists that include only the species most consistently present (recorded in >60% of releves for the community).

As illustrated in Fig. 3 and Table 3, functional differences between communities can be identified using species attributes that it is easy to measure and there is reasonable correspondence between the results of the FIBS analysis and the conclusions reached by RODWELL (National Vegetation Classification-calcareous grasslands and related vegetation types-internal Nature Conservancy Council document) based on extensive field knowledge of the vegetation types. However, cluster analysis, using data on plant strategies (Fig. 4), separates closely related phytosociological communities into different clusters. This suggests that phytosociologically similar communities may have very different management requirements.



The mean strategic composition of each cluster

strategy(% ± SD)	group I	group II	group III
C	0±0	0±0	3±1
S	66±5	46±5.	41±12
R	0±0	0±0	5±2
CR	0±0	0±0	3±4
SC	13±4	14±4	6±1
SR	6±4	0±0	6±7
CSR	15±7	42±1	37±5
	UNPRODUCTIVE	MORE PRODUCTIVE	MOST PRODUCTIVE

Fig. 3: A comparison of the strategic composition *sensu* Grime 1979 of related *Bromus erectus* sub-communities.
Conventions as in Fig. 2.

1.3.2. Identyfying potential threats to plant communities. In any releve the number of species that are infrequent in the community represented is often greater than the number of species that are frequent and characteristic of it. These least constant and uncharacteristic species, a numerically large but phytosociologically unimportant grouping, can also tell us something about the functional characteristics of the community.

If the ecological characteristics of the most constant (in >60% of samples) and of the least constant species of a community (≤20%) are dissimilar, the community may be unusually vulnerable to particular forms of vegetational change (or perhaps may even be already changing). Data for community CG3c illustrate this scenerio (Fig. 5). The least constant species of the community are more characteristic of derelict habitats than the most constant ones. This widespread occurrence of species of unmanaged habitats means that community CG3c will often have amongst its minor constituents species

TABLE 3.

Additional attributes and an independant ecological interpretation of the Bromus erectus *grassland communities illustrated in Figure 3.*

Data for regenerative characteristics showed little variation between sub-communities and have therefore been excluded.

	Community			
	3a	3b	3c	3d
Some attributes of species occuring at >60% constancy (from FIBS analysis)				
% species associated with rocky habitats	42	23	17	41*
% species with canopy heigh >300 mm.	0	8	23	8
% species characteristic of species poor (<18sppm^{-2}) vegetation	7	0	23	22
Characteristics of habitat of each NVC community (assessed by Rodwell, unpublished internal document for Nature Conservancy Council)				
Soil Type	shallow, calcareous renzina	intermediate between 3a and 3c	ceeper, mesotrophic brown rendizinas	as 3c
Management	lightly grazed or formerly grazed	vegetation more rank;? less recently grazed	mainly species of ranker mesotrophic? grassland	vegetation tall rank; originated after abandonment of arable land in absence of grazing

*-does not correspond with interpretation given by Rodwell.

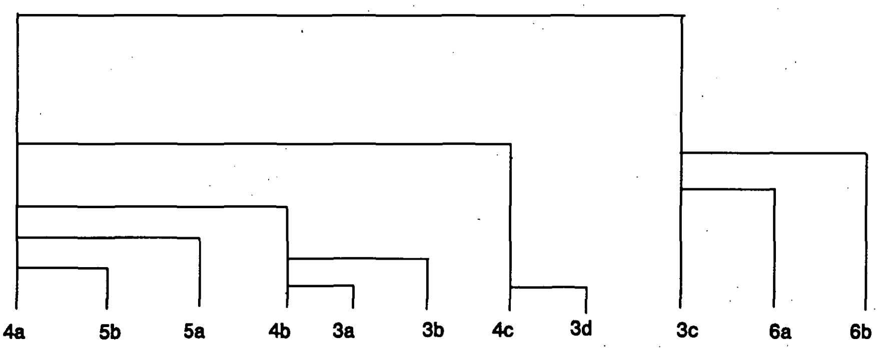


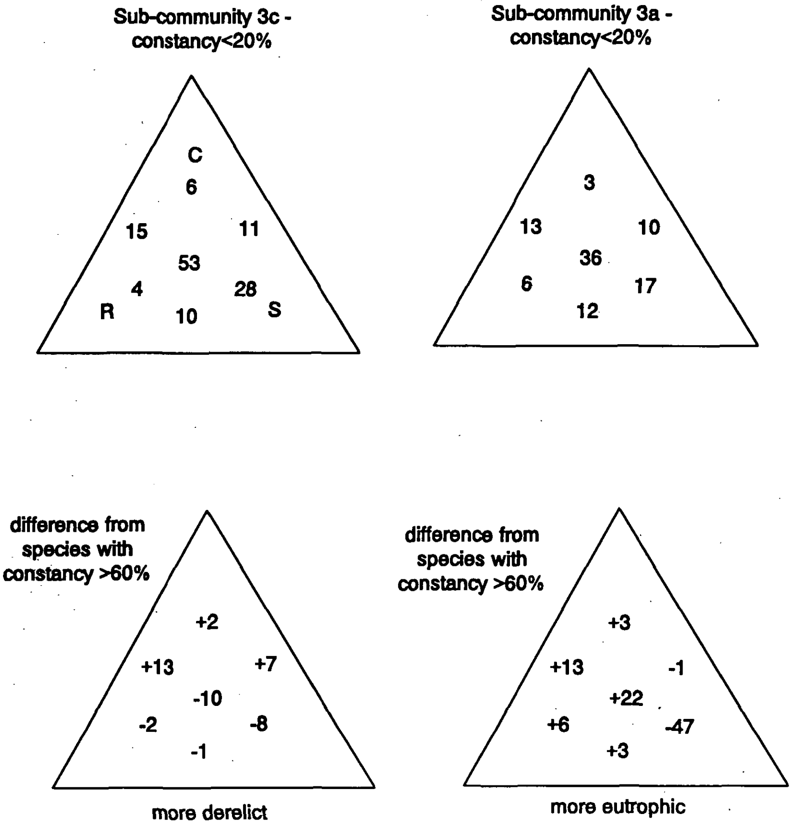
Fig. 4: Cluster analysis, using Ward's method, of the strategies *sensu* GRIME (1979) of *Bromus erectus* (CG 3a-d), *Brachypodium pinnatum* (CG 4a-c), *Bromus erectus-Brachypodium pinnatum* (CG 5a-b), and *Festuca rubra - Avenula pubescens* (CG 6a-b) grassland communities.

capable of expanding rapidly in the event of dereliction. Thus community CG3c is likely to be unusually responsive to dereliction (or may even already be changing as a consequence of it). For similar reasons the composition of community CG3a may change rapidly following eutrophication (Fig. 5).

2. Functional analysis of zoological datasets-commonness and rarity in animals

2.1. *Theoretical background*

Land-use appears to be the major determinant of the commonness and rarity of higher plants in the United Kingdom (HODGSON 1986 a-c, 1987). Species that exploit the productive and disturbed habitats produced as a consequence of modern agricultural, urban and industrial development are common while those restricted to the less productive habitats created by traditional agriculture are rare or decreasing. Habitat destruction is probably equally important in determining the abundance of animal species. Thus, the ecological attributes of common animals should parallel those for common plants and those for rare animals should be comparable to those for rare plants. Unfortunately, many animals are highly mobile with specialised requirements for feeding and for breeding. It is, therefore, often difficult even to identify the habitat requirements of animals let alone compare them. However, it is relatively easy to assess some features of life-history. Data are available in the literature describing life-history attributes of each British species for a number of different groups of animals. Furthermore, in Britain there is a long tradition, particularly amongst amateur naturalists, of recording the geographical distribution of animals and plants. The resulting distribution maps may be used to identify which species are widely distributed (common) and which have a restricted distribution (rare). This allows us through desk



% associated with:	constancy <20%	difference from high constancy species
wasteland	49	+12
spoil	26	+10
rocky habitats	17	0
arable	6	-9
pasture	45	-19
<18 spp m^{-2}	45	+22
canopy height >300mm	51	+28

% associated with:	constancy <20%	difference from high constancy species
arable	10	+10
spoil	27	+10
wasteland	45	+3
rocky habitats	12	-30
pasture	42	-40
<18 spp m^{-2}	45	+38
canopy height >300mm	50	+50

Fig. 5: A comparison of the strategic composition *sensu* Grime 1979 of the most constant (>60% of releves) and least constant (<20%) species in two *Bromus erectus* sub-communities.

studies to relate life-history attributes to commonness and rarity for a variety of invertebrate and vertebrate groups and to test the validity of predicted relationships between life-history attributes and abundance of the type presented in Table 4.

TABLE 4.

Key features of common and rare British habitats and the predicted life-history attributes of their associated animals. {It is assumed that commonness and rarity are largely determined by modern land-use and the conversion of unproductive habitats into productive and/or disturbed ones (see HODGSON 1986 a-c, 1987).}

HABITAT CHARACTERISTICS	Abundance		EXPECTED ATTRIBUETS OF ASSOCIATED FAUNA	Abundance	
	Common	Rare		Common	Rare
Productivity of habitat	high	low	growth-rate	high	low
Disturbance of habitat	often high	often low	% survival of adults from one year to the next	low	high
			number of offspring year^{-1}	high; may produce several generations year^{-1}	low; only one generation year^{-1}
			time to reproductive maturity	short	long

2.2. *Life history attributes of common and rare butterflies*

Butterflies are one of the simplest groups to analyse as the larvae of most British species feed on a single species or genus of food plant (Heath, Pollard & Thomas, 1984). The factors controlling the abundance of British butterflies also appear remarkably similar to those influencing the distribution of plants. Both plants from relatively productive habitats (competitors, competitive ruderals and CSR-strategists) and butterflies whose larval feed on *Urtica dioica* and *Pieris brassicae,* which eats *Brassica* spp.) tend to be common. In contrast, plants of less productive habitats (stress-tolerators, stress-tolerant ruderals and stress-tolerant competitors) and butterflies whose larvae eat plants with these strategies (e.g. *Hespera comma* feeding on *Festuca ovina* and *Lysandra bellargus* eating *Hippocrepis comosa)* are generally rare (Fig. 6).

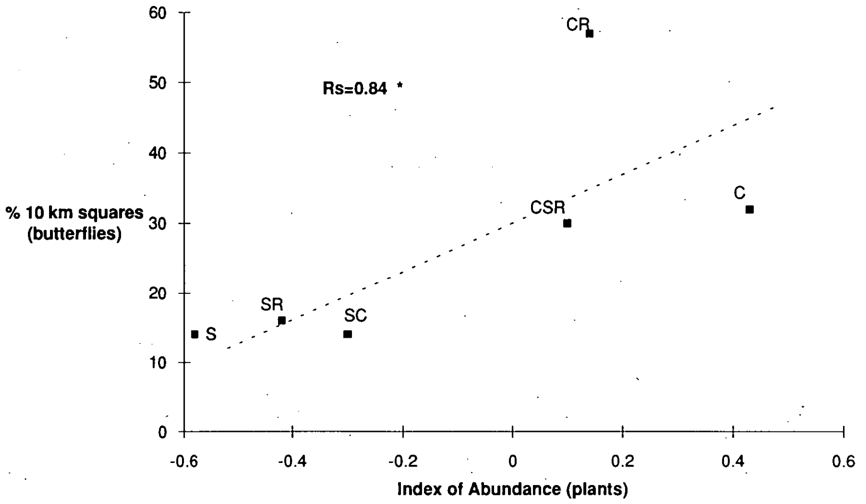


Fig. 6: The abundance of higher plants of different strategies *sensu* Grime (1974) in the Sheffield region compared to those of British butterflies grouped according to the strategy of their laval food plants.

$$\text{Index of Abundance} = \frac{\text{no. of common - no. of rare species}}{\text{total no. of species}}$$

It has a value of + 1 when all species are common and -1 when all species are rare. Strategies are abbreviated as in Fig. 1.

An association of the commonest butterflies with productive habitats is also illustrated by their tendency (a) to exploit larval food plants with a rapid growth rate (Fig. 7) and (b) to have a short-lived larval stage (Fig. 8a). In addition, many common butterflies form open mobile populations (Fig. 8b) and those exploiting competitive ruderal food plants may produce several broods each year (Fig. 8c). These attributes appear to allow common butterflies to colonise newly-created (productive) habitats and may render them less vulnerable to habitat disturbance or destruction. By contrast, the larvae of most rare butterflies eat slow-growing plants (Fig. 7) and are long-lived (Fig. 8a). Rare butterflies also tend to form non-mobile populations (Fig. 8b) and produce a single brood each year (Fig. 8c). Thus, rare butterflies, like rare plants (HODGSON, 1986 a-c, 1987), are, because of their life-history attributes, largely restricted to the less productive semi-natural habitats surviving from earlier, less intensive periods of land-use.

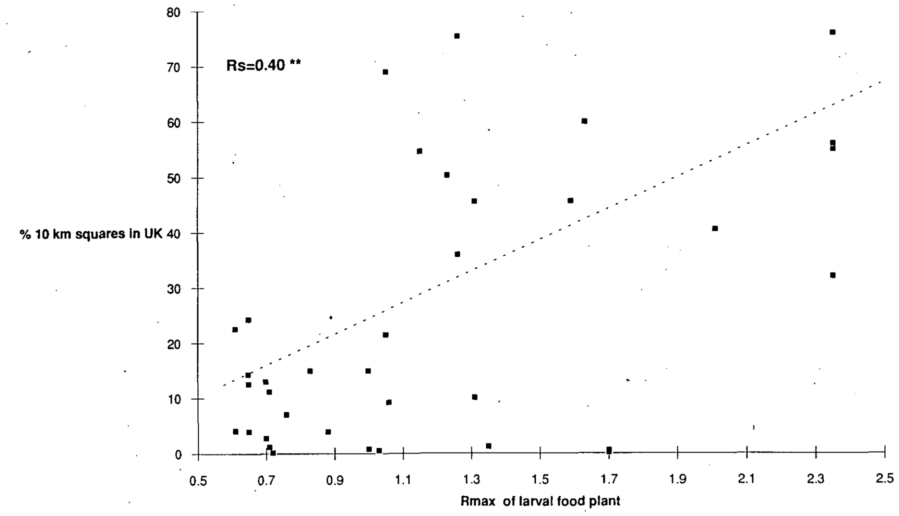


Fig. 7: The relationship between abundance of British butterflies and the R_{max} of their larval food plants (from HODGSON, in press).

2.3. *Life-history attributes of common and rare British birds*

Birds have complex habitat requirements for nesting and feeding and the level of productivity and disturbance within their complex and heterogeneous breeding habitat often cannot readily be assessed by reference to botanical data. Thus data for birds are less readily interpreted than those for butterflies. However, relationships between life-history attributes and abundance can be identified for British birds. As summarized in Table, small common birds (e.g. *Passer domesticus)* tend to produce several broods each year and to attain early reproductive maturity while small rare birds may produce only one brood per year and take longer to become reproductively mature (e.g. *Hydrobates pelagicus).* This suggests that small common birds tend to

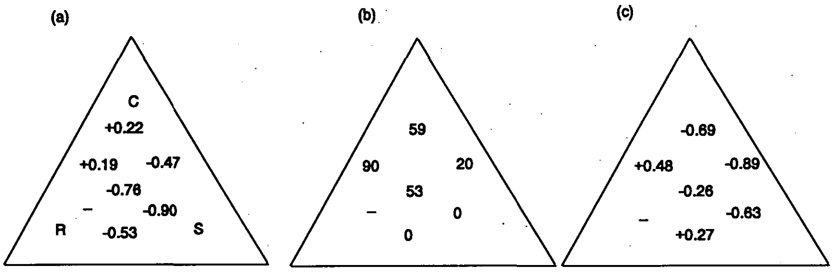


Fig. 8: The relationship between the life-history attributes of British butterflies and the strategy *sensu* Grime (1974) of their larval food plants (from Hodgson, in press).

(a) estimate of relative

$$\text{duration of adult and larval stage} = \frac{\text{no. of spp. with } A>2 \times L - \text{no. of spp. with } L>2 \times A}{\text{total no. of spp.}}$$

(A and L represent the duration of the adult and larval stages respectively)
(b) % of species forming open, mobile populations
(c) no of broods y^{-1}

$$\text{Estimate for no. of broods} = \frac{\text{no. of spp.} >2 \text{ broods } y^{-1} - \text{no. of spp with 1 brood } y^{-1}}{\text{total no. of spp.}}$$

exploit productive but disturbed habitats and that small rare birds are restricted to unproductive habitats (see Table 4). Larger common birs (e.g. *Corvus corone)*, tend to reach reproductive maturity early and to produce eggs with a short period of incubation (Table 5). They also tend to be associated with more productive habitats. By contrast, many larger rarer birds (e.g. *Aquila chrysaetos)* tend to grow more slowly (Table 5) and may be restricted to less productive habitats.

Table 5.

Summary of the differences between common and rare British birds - from Hodgson *(in preparation). Data on life-history attributes were abstracted from* Perrins *(1987) and on breeding distribution from* Sharrock *(1976).*

	small (<30 g.)		large (>500 g.)	
	common	rare	common	rare
No. eggs clutch^{-1}	5-7	<5 or >7	no clear trends	
No. of broods (year^{-1})	≥2	1	1	1
Age when first breeds (year^{-1})	1	≥2	1	≥2
Incubation time (days)	≤14	>14	≤21	≥28
Prefered food	no clear trends		animal + plant	animal

It must be stressed that the relationships described above are closely related to phylogeny. Life-history attributes are strongly correlated with higher-order taxonomic units (HARVEY & PAGEL, 1991). Thus, species are predisposed to commonness or rarity simply because of the evolutionary grouping to which they belong. Orders such as Passeriformes tend to contain many common species while Acciptiriformes include several endangered species.

2.4. *Life-history attributes of Spanish birds from contrasted habitats*

As will be illustrated using data from the Leon uplands, Spain (REBOLLO, unpublished; Table 6), life-history attributes are also related to habitat quality. All but the woodland habitats identified by REBOLLO can readily be separated by reference to two factors, (a) their agricultural productivity, which is likely to affect the amount and quality of food available and (b) their level of disturbance (Table 7). Disturbance relates both to impacts that affect the whole habitat (e.g. ploughing, burning and grazing) and to effects where the destruction of biomass is more specific, i.e. through predation. It is assumed that the risk of predation is greater in low-growling vegetation, where cover and secure nest and roosting sites are scarce and birds are more visible. As illustrated in Table 8 and summarized in Figure 9, the nidicolous birds of pasture, a disturbed, relatively unproductive habitat, those of agricultural habitats around villages (productive, disturbed) and those of rocky ground (unproductive, less disturbed) differ in their life-history attributes. These differences accord with ecological theory. As predicted by GRIME (1979) for plants, even small birds of (unproductive) rocky habitats tend to be slow to develop into fledglings. Also as expected, birds from both productive disturbed

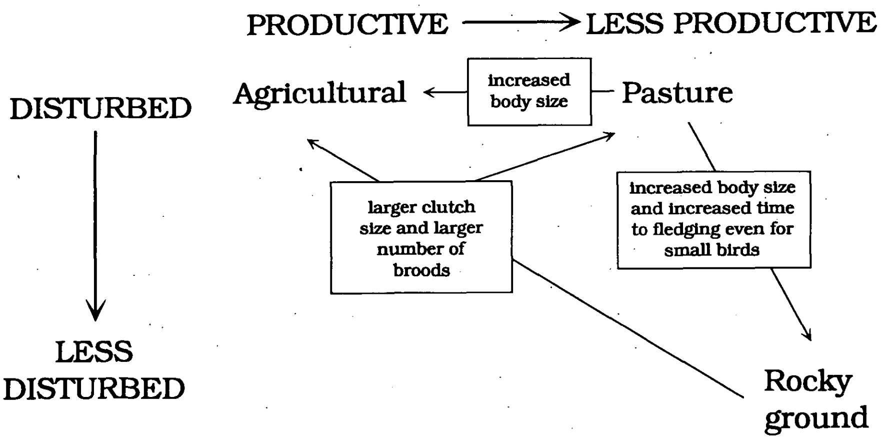


Fig. 9: Summary of differences in the life-history attributes of birds identified in Table 8 and their relation to habitat characteristics.

TABLE 6.

The birds nesting in different habitats in the uplands near Leon, Spain.
Data from Rebollo (unpublished).
pl, pu, wl and wu indicate respectively nestin only in lower (900-1.300 m.) pasture, upper (1.300-1.700 m.) pasture, lower woodland and upper woodland and birds from the agricultural habitat identified by 'v' typically nest in buildings.
Species were omitted from the subsequent principal component analysis if they were, nidifugous; ^{1}, a brood parasite or $^{+}$, if insufficient life-history data were available.*

Agricultural only: -Apus apus (v), Athene noctua (v), Ciconia ciconia (v), Cinclus cinclus, Columba livida (v), Hirundo rustica (v), Otus scops (v), Passer domesticus (v); Passer montanus (v), Pica pica, +Sturnus unicolor (v), Tyto alba (v).

Pasture only: -Alauda arvensis, *Alectoris rufa, $^{+}$Anthus campestris, Circus cyaneus, Circus pygargus, *Perdix perdix, Saxicola rubetra (pu), Sylvia cantillans (pl), Sylvia undata.

Rocky ground only: -Apus melba, Aquila chrysaetos, Falco peregrinus, Monticola solitaris, Montifringillia nivalis, Neophron percnopterus, Ptyonoprogne rupestris, Pyrrhocorax graculus, Pyrrhocorax pyrrhocorax, Tichodroma muraria.

Woodland only: -Accipiter gentilis, Accipiter nisus, Buteo buteo, *Caprimulgus europaeus, Certhia familiaris (wu), Circaetus gallicus, Dendrocopos minor (wu), Dryocopus martius (wu), Milvus migrans, Milvus milvus, Parus palustris, Pernis apivorus (wu), Phylloscopus trochilus (wu), Regulus regulus, *Scolapax rusticola (wu), Sitta europaea, Streptopelia turtur (wl), Strix aluco, *Tetrao urogallus (wu), Troglodytes troglodytes, Turdus philomelos, Upupa epops (wl).

Agricultural and pasture: -Carduelis carduelis (pl), *Coturnix coturnix, Emberiza calandra (pl), Jynx torquilla (pl), Lanius collurio, Motacilla alba (pu), Saxicola torquata.

Agricultural and rocky ground: -Delichon urbica.

Agricultural and woodland: -Chloris chloris, Coccothraustes coccothraustes (wl), $^{+}$Petronia petronia (wl).

Pasture and rocky ground: -Anthus spinoletta (pu), Monticola saxatilis, Oenanthe oenanthe, Prunella collaris (pu).

Pasture and woodland: -^{1}Cuculus canorus (pl), Emberiza hortulana (wl), Ficedula hypoleuca (pl), Lullula arborea (pl, wl), Parus ater, Parus cristatus (pl), Phoenicurus phoenicurus (pl, wl).

Agricultural, pasture and rocky ground: -Motacilla cinerea (pu), Phoenicurus ochrurus.

Agricultural, pasture and woodland: -Aegithalos caudatus, Anthus trivialis, Carduelis cannabina, Certhia brachydactyla (pl), Columba palumbus (pl), Corvus corone (pl), Dendrocopos major (pl), Emberiza cia, Emberiza citrinella (pu), Erithacus rubecula, Falco tinnunculus (pl, wl), Fringilla coelebs, Garrulus glandarius, Hippolais polyglotta (pl, wl), Luscinia megarhynchos (pl, wl), Parus caeruleus, Parus major, $^{+}$Phylloscopus bonelli (pl), Phylloscopus collybita (pl), Picus viridis (pl, wl), Prunella modularis, Pyrrhula pyrrhula (pl), Regulus ignicapillus (pl), Serinus serinus, Sylvia atricapilla, Sylvia borin, Sylvia communis (wl), Turdus merula, Turdus viscivorus.

Pasture, rocky ground and woodland: -Corvus corax (pl, wl).

TABLE 7.

The presumed level of productivity and disturbance associated with three bird habitats in the Leon uplands, Spain.

Habitat	Status	Comments
1. Agricultural (Village, Meadow and Arable)	disturbance - moderate productivity - high	major acts of human disturbance but building may provide secure sites for breeding and human persecution of top carnivores (% survival of adults y^{-1} 62±22, no of species for wihich data available 5); the most productive area at least in agricultural terms.
2. Pasture	disturbance - high productivity - moderate	sites disturbed by grazing and little tall cover and few breeding large birds to nest (56±17, 5); site productivity intermediate between 1 adn 3.
3. Rocky ground	disturbance - low productivity - low	ledges and crevices may provide secure sites for nesting (73±9, 2) but little biomass

TABLE 8.

The life-history attributes (± standard deviation) of birds from different habitats in the Leon uplands, Spain. Species lists and life-history attributes were abstracted from Rebollo (unpublished data) and Perrins (1987) respectively. Sites differ in their level of agricultural production and this analysis explores the relationship between life-history attributes and site productivity. Accordingly in I bird species have been ascribed to the least productive habitat in which they breed and in II only species restricted to rocky habitats are included.

land-use (ordered by decreasing productivity)	*no of species*	*body weight (g)*	*minimum incubation time* (days)	*minimum fledging time* (days)	*maximum eggs brood*$^{-1}$	*no.of broods y*$^{-1}$
I. GRASSLAND AND RELATED HABITATS						
1 Agricultural (villages, small cultivated areas and meadows; nesting in buildings)						
(a) 900-1.300m.	15	311±820	18±7	25±14	5.3±1.4	1.9±0.8
2 Pastoral (pastures, scrub and scattered trees)						
(a) 900-1.300m.	20	149±285	15±4	18±8	6.1±1.8	1.6±0.6
(b) 1.300-1.700m.	38	61±104	14±4	18±15	6.9±3.2	1.7±0.5
Mann-Whitney *U* test						
1 *v.* 2a		z=-1.75^1 P<0.1	z=-1.23 NS	z=1.79 P<0.1	z=-1.24 NS	z=-1.11 NS
1 *v.* 2b		z=-2.74^1 **	z=-2.20 *	z= 2.79 **	z=-1.00 NS	z=-0.53 NS
2a *v.* 2b		z=-0.09 NS	z=-1.03 NS	z=-0.83 NS	z=-0.21 NS	z=-1.18 NS
Spearman Rank Correlation between life-history attributes						
v. body weight			R_s=+0.56 ****	R_s=+0.53 ***	R_s=-0.13^1 NS	R_s=-0.25 *
v. minimum incubation time			R_s=+0.80^3	R_s=+0.17^1 ***	R_s=-0.39 P<0.1	***
v. minimum time to fledging				R_s=+0.24^3	R_s=-0.36 *	***
v. maximum no. eggs brood^{-1}				R_s=-0.32^1		**
II ROCKY HABITATS ONLY						
(a) (900-1.700m.)	10	805±1.419	22±12	38±23	3.9±1.2	1.2±0.4
Mann-Whitney *U* test						
1 *v.* II		z=-1.00 NS	z=-1.09 NS	z=-1.88 P<0.1	z=-2.71 **	z=-2.11 *
2a *v.* II		z=-2.24 *	z=-2.11 *	z=-3.10^2 **	z=-3.32 ***	z=-1.59 NS
2b *v.* II		z=-2.88 **	z=-3.00 **	z=-3.80^2 ***	z=-4.22^1 ***	z=-2.73 **

[1], [2], [3], - statiscally significant difference at P<0.05, P<0.01 and P<0.001 level respectively when larger birds (>50 g.) were excluded. For 1 v II, 2a v II and 2b v II n=12, 18 and 34 respectively. Small birds were separated (a) to lessen the influence of body size on other attributes and (b) because small birds are perhaps likely to obtain more of their food close to their nest site.

habitats (agricultural) and less productive ones (pasture), tend to have larger clutch sizes and to produce more broods each year than those of less disturbed, less productive rocky ground. These latter results are also in accordance with the earlier theory of r- and K-selection (PIANKA 1970).

The relationship between body size and habitat stress cannot be assessed adequately from this dataset. The larger body weight of many village birds may be a reflection of the fact that the habitat is rich in food resources (and nesting sites). Larger animals have higher requirements for energy (WOOD 1983). However, larger size may also be a symptom of an unfavourable habitat. Food accumulated in storage tissue allows survival of short-term food shortages. A further complication is that many larger birds utilize secure nest sites within otherwise stressed rocky habitats but feed elsewhere, perhaps in rather more productive habitats.

The use of the discriminatory life-history attributes described above in a principal component analysis allows a tentative classification of functional types for both individual species and for avian faunas (Figs. 10-11). However, the results should be treated with caution. Firstly, the data deal with the distribution of species in summer, when the distribution of species will be determined by requirements for both nesting and feeding. With hindsight, it would have been better to analyse distributional patterns during winter, when distribution will be primarily determined by feeding requirements. Secondly, the analyses are only qualitative. The small birds from Passiformes are particularly well represented in the dataset. Had estimates of biomass based upon population size been available rather than presence/absence data, the results in Fig. 11 would have been different. Thirdly, the absence of lists from a productive undisturbed habitat and the lack of growth rate data to provide a direct assessment of habitat productivity inevitably restricts the value of the classification presented. Studies of this type have tended to concentrate on relationships such as those between growth rate and body weight or time to fledging (RICKLEFS 1968, 1973). Some (e.g. PONTIER *et. al.,* 1990) have shown that many other important life-history attributes and ecological characteristics are also interrelated. However, the possible importance of habitat quality has been largely ignored. Until the relationships between habitat quality and life-history attributes are studied more fully, CSR strategy theory (GRIME 1979) will inevitably have many fewer adherents among zoologists than theories such as that or r- and K-selection (PIANKA 1970).

3. Conclusions

This paper describes a two-phased analysis of plant and animal species lists. The first stage involves the simplification of the data by replacing species, of which there are c. 6.000 in the Spanish flora, by functional attributes for which the number of character states possible is much smaller. The second stage provides an interpretation, based upon ecological theory, of this newly created set of functional data. Inevitably there are still problem areas. For example, for plants (Table 1) and even more for animals (Tables 4 and 6) few attributes relating to growth-rate are readily available to assess site productivity. Tests are also needed to assess the effectiveness of FIBS in interpreting floristic changes to woody vegetation, where differences in regenerative strategy may be as important as features of the established plant in determining success or failure of species. More basically, physiological data for testing strategy theory are required (see Appendix of Grime *et al*, 1988). These are presently being collected at Sheffield as part of the Integrated Screening Programme. Also, this type of analysis does not, at least at present, identify changes caused by pollutants such as pesticides and SO_2. Nevertheless, the method may, in time, allow the life-history attributes of animals and plants co-existing in the same ecosystem to be compared and may eventually lead, as suggested by Figs 10 and 11, to classifications of life-history that can encompass both animals and plants. At a more inmediate and practical level, FIBS also appears to provide sensible answers to questions related to land management and conservation and could readily be modified to be relevant to climate warming. Indeed, the main advantage of FIBS is that it can be utilized now at a time when habitats of great scientific interest are being destroyed. I look forward to taking part with other ecologists in an attempt to apply FIBS to field situations in Catalonia and nearby in the Pyrenees. I hope that this will both assist in the conservation of the floristic and faunistic diversity of the region and, by applying them to field situations, help to refine the ecological theories underpinning FIBS.

Acknowledgements

This work draws heavily upon ecological theories developed by Professor Philip Grime and on floristic data jointly collected with Professor Grime and Dr. Rod Hunt. I would also like to thank Dr. Salvador Rebollo for providing the Spanish bird data, Javier Alvarez for permission to visit the experimental plots at Piedrafita, to Drs. Gabriel and Josep Montserrat Martí, Dr. Angel Romo, Dr. Antonia Julia, Dr. Miguel Angel Rodriguez, Dr. Lluis Torres, Javier Alvarez, Dr. Choni Garcia and for permission to include jointly collected data, to English Nature for permission to utilize phytosociological data, to Ric Colasanti for help in data analysis and to Andreas Stockey and Dr. Sandra Díaz for translating the summary. The manuscript has been improved as a result of the comments of Drs. Tim Birkhead, Gabriel Montserrat Martí, Salvador Rebollo and Ken Thompson. This was supported by the National Environment Research Council and the Spanish fieldwork carried out while a guest of the Asociación Española de Ecología Terrestre.

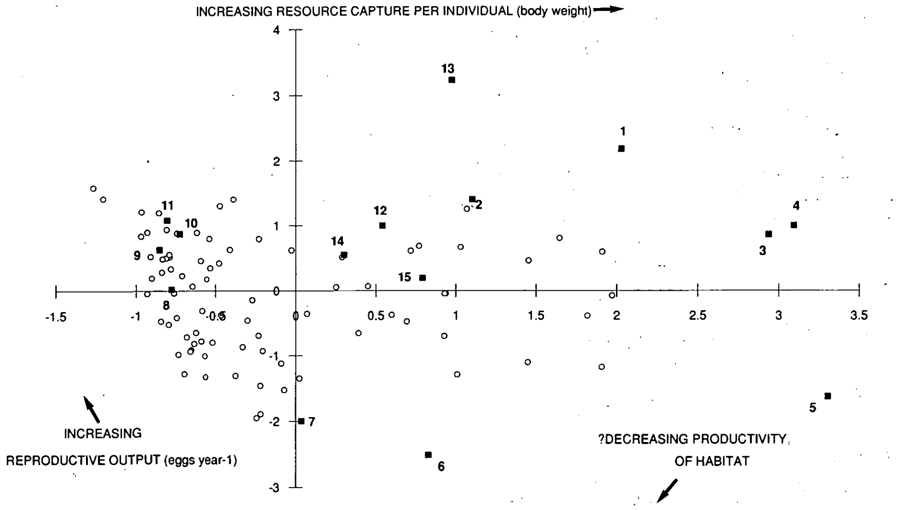


Fig. 10: Principal component analysis, and a strategic interpretation, of some life-history attributes for nidicolous birds of the Leon uplands, Spain.

Life-history attributes included in the PCA were $\log_{10}$ maximum body weight, $\log_{10}$ number of eggs y^{-1} and minimum time from egg-laying to fledging.

Species identified on the diagram:

	body weight (g)	incubation time (days)	time to fledge eggs (days)	brood^{-1}	broods y^{-1}
Possibly analagous to competitors in plants					
1. Ciconia ciconia	3.000-3.500	33-34	58-64	3-5	1
2. Corvus corax	800-1.500	21	35-40	4-6	1
Possiby analagous to stress-tolerant competitors in plants					
3. Aquila chrysaetos	2.850-6700	43-45	65-70	2	1
4. Neophron percnopterus	1.600-2.200	42	90-95	2	1
Possibly analagous to stress-tolerators in plants					
5. Circaetus gallicus[1]	1.100-2.300	45-47	70-75	1	1
6. Apus apus[2]	36-50	18-25	37-56	2-3	1
Possibly analagous to stress-tolerant ruderals in plants					
7. Tichodroma muraria[2]	15-20	18-19	21-26	4	1
8. Parus caeruleus[3]	9-12	13-14	18-20	6-12	1
Possibly analagous to ruderals in plants					
9. Erithacus rubecula	16-22	13-14	12-15	4-6	2(3)
10 Hirundo rustica	16-25	14-16	17-21	4-6	2(3)
11. Passer domesticus	22-32	12-14	14-16	3-6	2-3
Possibly analagous to competitive ruderals in plants					
12. Columba livida	240-300	16-19	35-37	2	3 or more
13. Tyto alba	290-460	30-32	55-65	4-7	1-2
Possibly analagous to CSR-strategists in plants					
14. Pica pica	200-250	17-18	22-27	5-7	1
15. Falco tinnunculus	190-300	27-29	27-32	3-6	1

[1], [2] and [3] indicate respectively possibly intermediate between stress-tolerant competitor and stress-tolerator, between stress-tolerator and stress-tolerant ruderal and between stress-stress-tolerant ruderal and ruderal.

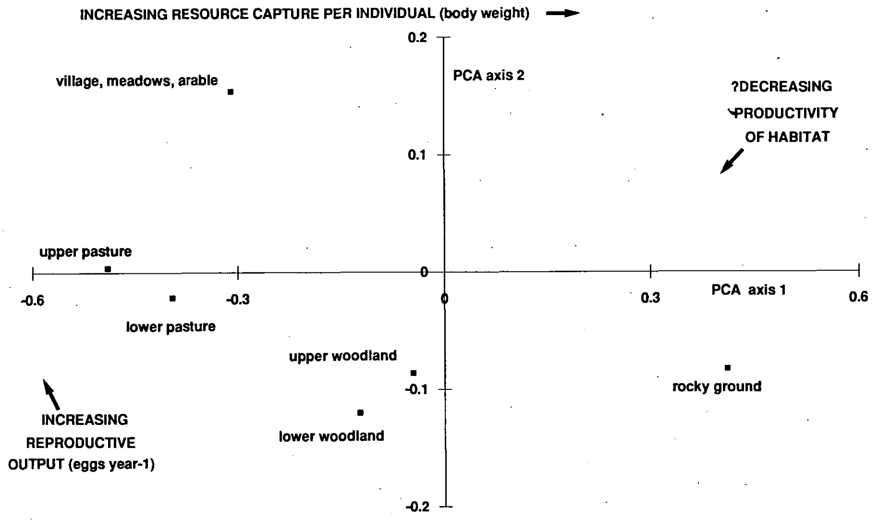


Fig. 11: The life-history characteristics of the avian fauna of different habitats in the Leon uplands, Spain expressed as mean values on the first two axes of the Principal Component Analysis described in Fig. 10.

Life history attributes analysed were $\log_{10}$ maximum body weight, $\log_{10}$ number of eggs y^{-1} and minimum time from egg-laying to fledging. Statistically significant differences at $P<0.05$ level identified using the Mann-Whitney *U* test are denoted by a suffix that identifies the number of the other habitat being compared. Unlike Table 8, in which an attempt was made to identify ecological differences between habitats, this analysis is strictly descriptive and species were assigned to all the habitats in which they occurred. Thus, for example, the list for habitat 1 now includes birds that nest both on rocky ground and in other habitats and that for habitat 6 does not exclude birds that do not nest in buildings.

Habitats identified on the diagram:-

	no of species	body weight (g)	time from egg laying to fledging		maximum number of eggs y^{-1}	
			all species	≤50 g.	all species	≤50 g.
1. Rocky ground	18	507±1.083$^{3-6}$	48±29^{3}	31±5$^{3-6}$	7.2±4.0$^{4-6}$	10±3
2. Upper woodland	44	203±326	37±18^{5}	27±4	8.9±4.2	11±4
3. Lower woodland	49	147±260	35±16	27±4	9.1±4.0	11±4
4. Lower pasture	49	98±204	31±11	26±3	9.7±3.5	11±3
5. Upper pasture	35	51±92	28±10	26±3	10.4±3.2	11±3
6. Village, meadows, arable	50	143±464	31±15	27±6	10.2±4.0	11±4

References

BOLOS, O. (1967): Comunidades vegetales de las comarcas próximas al litoral entre los ríos Llobregat y Segura. *Mem. Real Acad. Cienc. Artes Barcelona,* 38(1): 1-269.

BRAUN-BLANQUET, J. & BOLOS, O. (1957): Les groupements vegetaux du Bassin de l'Ebre. *Anales Est. Exp. Aula Dei.* 5 (1-4): 1-266.

FROHAWK, F. W. (1934): *The Complete Book of British Butterflies.* Ward & Lock, London.

GRIME, J. P. (1986): Manipulation of Plant Species and Communities. In A. D. BRADSHAW, E. THORPE & D. A. GOODE (Eds). *Ecology and Design in landscape,* 175-194.

GRIME, J. P. (1979): *Plant Strategies and Vegetation Processes.* John Wiley & Sons, Chichester.

GRIME, J. P., HODGSON, J. G., & HUNT, R. (1988): *Comparative Plant Ecology: A Functional Approach to Common British Plants.* Unwin Hyman, London.

HARVEY, P. H. & PAGEL (1991): *The comparative method in evolutionary biology.* Oxford University Press, Oxford.

HEATH, J., POLLARD, E. & THOMAS, J. A. (1984): *Atlas of Butterflies in Britain & Ireland.* Viking, London.

HODGSON, J. G. (1986) a): Commonness and rarity in plants with special reference to the Sheffield flora. I. The identity, distribution and habitat characteristics of the common and rare species. *Biological Conservation,* 36(3): 199-252.

HODGSON, J. G. (1986) b): Commonness and rarity in plants with special reference to the Sheffield flora. II. The relative importance of climate, soils and land use. *Biological Conservation,* 36(3): 253-284.

HODGSON, J. G. (1986) c): Commonness and rarity in plants with special reference to the Sheffield flora. III. Taxonomic and evolutionary aspects. *Biological Conservation,* 36(3), 275-296.

HODGSON, J. G. (1987): Growing rare in Britain. *New Scientist,* 113 (1547): 38-39.

HODGSON, J. G. (1989): The use of autecological information for selecting and managing plant materials used in habitat construction and the creation of species-rich vegetation. In G. P. BUCKLEY (Ed.) *Habitat reconstruction, transplantation and repair.* Bellhaven Press, London, 45-67.

HODGSON, J. G. (1990): The role of autecological accounts in calcareous grasslands. In S. H. HILLIER, D.W.H. WALTON & D. WELLS (Eds.) *Calcareous Grasslands - Ecology and Management.* Bluntisham Books, Huntingdon, 161-168.

HODGSON, J. G. (1991): Management for the conservation of plants with particular reference to the British flora. In I. F. SPELLERBERG, F. B. GOLDSMITH & M. G. MORRIS (Eds.) *The Scientific Management of Temperate Communities for Conservation.* Blackwell, Oxford, 81-102.

HODGSON, J. G. (in press): Commonness and rarity in British butterflies. *Journal of Applied Ecology* (in press).

LASANTA-MARTÍNEZ, T. (1988): The process of desertion of cultivated areas in the Central Spanish Pyrenees. *Pirineos,* 132: 15-36.

LASANTA-MARTÍNEZ, T. (1990): Tendencias en el estudio de los cambios de uso del suelo en las montañas españolas. *Pirineos,* 135: 73-106.

PERRINS, C. (1987): *New Generation Guide to the Birds of Britain and Europe.* William Collins, London.

PIANKA, E. R. (1970): On r- and K-selection. *American Naturalist,* 104: 592-597.

PIENADO LORCA, M. & RIVAS-MARTÍNEZ, S. (eds.) (1987): *La vegetación de España.* Univ. de Alcalá, Madrid.

PONTIER, D., ALLAINE, D., TROUVILLEZ, J., CLOBERT, J., GAILLARD, J. M. & LEBRETON, J. D. (1990): Are the demographic patterns of birds related to biological and environmental parameters? In J. Maynard Smith & G. Vida (Eds.) Organizational constraints on the dynamics of evolution, pp. 311-320. Manchester University Press, Manchester.

RICKLEFS, R. E. (1968): Patterns of growth in birds. *Ibis,* 110: 419-451.

RICKLEFS, R. E. (1973): Patterns of growth in birds. II. Growth rate and mode of development. *Ibis,* 115: 177-201.

RIVAS MARTÍNEZ, S., DÍAZ, T. E., FERNÁNDEZ PRIETO, J. A., LOIDI, J. & PENAS, A. (1984): *La vegetación de la alta montaña cantábrica: los Picos de Europa.* Ed. Leonesas, León.

RODWELL, J. (1991): *British Plant Communities.* Volume 1. *Woodland and scrub.* Cambridge University Press, Cambridge.

THOMAS, J. A. (1984): The conservation of butterflies in temperate countries: past efforts and lessons for the future. In R. I. VANE-WRIGHT & P. R. ACKERY (Eds.) *The Biology of Butterflies. Symposium of the Royal Entomological Society of London, 11,* 333-353.

WOOD, J. B. (1983): The conservation and management of animal populations. *Conservation in Perspective* (Ed. by A. Warren & F. B. Goldsmith), pp. 119-139. Wiley, Chichester.