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Partitioning selection and complementarity in biodiversity experiments

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The impact of biodiversity loss on the functioning of ecosystems and their ability to provide ecological services has become a central issue in ecology. Several experiments have provided evidence that reduced species diversity may impair ecosystem processes such as plant biomass production^{1–5}. The interpretation of these experiments, however, has been controversial^{6–12} because two types of mechanism may operate in combination^{6,13–15}. In the 'selection effect', dominance by species with particular traits affects ecosystem processes. In the 'complementarity effect', resource partitioning or positive interactions lead to increased total resource use. Here we present a new approach to separate the two effects on the basis of an additive partitioning analogous to the

Price equation in evolutionary genetics^{16–19}. Applying this method to data from the pan-European BIODEPTH experiment⁴ reveals that the selection effect is zero on average and varies from negative to positive in different localities, depending on whether species with lower- or higher-than-average biomass dominate communities. In contrast, the complementarity effect is positive overall, supporting the hypothesis that plant diversity influences primary production in European grasslands through niche differentiation or facilitation.

Recent theoretical work has revealed that the observed responses of ecosystem processes to changes in species or functional-group diversity can be generated by a combination of different effects^{13–15}. These biodiversity effects can be grouped into two classes. First, there are those that arise from niche differentiation or facilitation between species, and that can increase the performance of communities above that expected from the performance of individual species. Distinguishing the effects of niche differentiation and facilitation may often be difficult in practice; therefore, we refer to these mechanisms collectively as 'complementarity'. One common form of complementarity in plant communities (which involves both resource partitioning and facilitation) arises between legumes, which have the ability to fix atmospheric nitrogen, and other plants, which have access only to soil nitrogen.

The second class of biodiversity effects gives rise to relationships between biodiversity and ecosystem functioning through selective processes, such as interspecific competition, which cause dominance (high relative abundance) of species with particular traits. For example, in one model of the 'sampling effect'^{6,13}, higher-diversity plant mixtures assembled at random from a pool of species have a higher chance of containing and becoming dominated by the

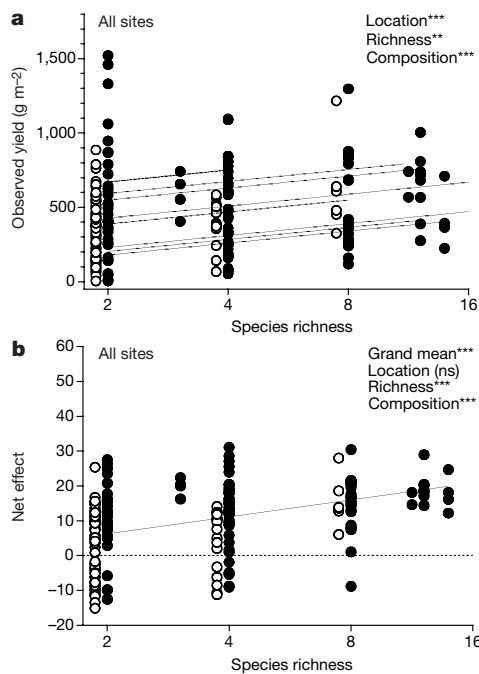


Figure 1 Observed yield Y_0 and net biodiversity effect ΔY as functions of species richness across all localities in mixtures of the BIODEPTH experiment. **a**, Observed yield; **b**, net biodiversity effect. Open circles are plots that do not contain any legume species; filled circles are plots that contain legumes. Lines are slopes from the multiple regression model using species richness on a \log_2 scale. Lines in **a** from highest elevation to lowest are: Germany, Silwood, Sheffield, Switzerland, Ireland, Greece, Sweden and Portugal. Values of the biodiversity effect (in g m^{-2}) are square-root transformed to meet the assumptions of analyses but preserve the original positive and negative signs. (Single asterisk, $P < 0.05$; double asterisk, $P < 0.01$; triple asterisk, $P < 0.001$; ns: non-significant.)

species that achieves the highest biomass when grown alone. The model assumes that the biomass of a mixture of species is equal to the monoculture biomass of the most productive of the component species.

Although both types of effect are potentially relevant, they have different implications and may apply to different circumstances¹⁵.

Box 1

Additive partition of biodiversity effects

We measure the net biodiversity effect, ΔY , by the difference between the observed yield of a mixture and its expected yield under the null hypothesis that there is no selection effect or complementarity effect. This expected value is the weighted (by the initial relative abundance of species in mixture) average of the monoculture yields for the component species. Positive selection occurs if species with higher-than-average monoculture yields dominate the mixtures. The selection effect is measured by the covariance between the monoculture yield of species and their change in relative yield in the mixture. Finally, a positive complementarity effect occurs if species yields in a mixture are on average higher than expected on the basis of the weighted average monoculture yield of the component species. These various effects can be related by additive partition as follows.

Define, for any mixture,

- M_i = yield of species i in monoculture
- Y_{O_i} = observed yield of species i in the mixture
- $Y_o = \sum_i Y_{O_i}$ = total observed yield of the mixture
- RY_{E_i} = expected relative yield of species i in the mixture, which is simply its proportion seeded or planted
- $RY_{O_i} = Y_{O_i}/M_i$ = observed relative yield of species i in the mixture
- $Y_{E_i} = RY_{E_i}M_i$ = expected yield of species i in the mixture
- $Y_E = \sum_i Y_{E_i}$ = total expected yield of the mixture
- $\Delta Y = Y_o - Y_E$ = deviation from total expected yield in the mixture
- $\Delta RY_i = RY_{O_i} - RY_{E_i}$ = deviation from expected relative yield of species i in the mixture
- N = number of species in the mixture

It then follows that

$$\Delta Y = Y_o - Y_E = \sum_i RY_{O_i}M_i - \sum_i RY_{E_i}M_i = \sum_i \Delta RY_i M_i$$

$$= N \overline{\Delta RY} \overline{M} + N \text{cov}(\Delta RY, M)$$

In this equation, $N \overline{\Delta RY} \overline{M}$ measures the complementarity effect, and $N \text{cov}(\Delta RY, M)$ measures the selection effect.

Note that this approach is a generalization of the relative yield total (RYT) and proportional deviation from expected value (D) approaches^{21,22}. Indeed, $N \overline{\Delta RY} = \text{RYT} - 1 = \overline{D}$ and $\Delta Y = D_T Y_E$. Thus, the above equation can be rewritten as $D_T Y_E = \overline{D} \overline{M} + N \text{cov}(\Delta RY, M)$ from which it is apparent that the net biodiversity effect is proportional to D_T , and the complementarity effect is proportional to \overline{D} .

As a consequence, our method has similar strengths and limitations to these approaches. Relative yield has traditionally been used in short-term plant competition experiments with substitutive designs in which total density is kept constant (as was the case in BIODEPTH). Results may then be dependent on the chosen density^{11,20}, although they seldom vary strongly in practice^{12,25}. Our approach, however, could be applied to other organisms and other experimental designs in which density is allowed to reach natural levels. As it is based on variation in relative yield (ΔRY), it could also be used to study how biodiversity effects change through time, by comparing observed values at each time with expected values calculated either from initial conditions or from the conditions of the previous time. □

Much of the controversy over recent experiments has revolved around the significance of the sampling effect and its contribution to the observed responses to experimental manipulations of biodiversity^{6–12}, prompting the need for methods to separate the sampling effect from complementarity^{20–22}. The sampling effect model, however, has restrictive assumptions which do not qualify it as a general alternative to complementarity. First, communities may not be dominated by a single species, and relative abundance and the magnitude of impact on ecosystem functioning may not be positively correlated. In particular, a negative selection effect can arise if communities are dominated by species with low—not high—values for a particular trait or process^{14,15,23}. Second, the sampling effect model actually combines two different processes: a sampling process and an extreme selection process that favours the single most productive species. The sampling process is shared by the selection and complementarity mechanisms: in both cases, communities that have more species also have a greater probability of containing the appropriate species (either single species with particular trait values or a combination of species with complementary traits). Thus selection, not sampling, really distinguishes the two classes of mechanism¹⁵. This strengthens the need for more general, conceptually clear methods that can identify their individual contributions in biodiversity experiments.

Our new methodological approach meets this need by providing an additive partitioning of two biodiversity effects: a ‘selection effect’ and a ‘complementarity effect’ (Box 1). The selection effect is based on Price’s general theory of selection²⁴: selection occurs when changes in the relative yields of species in a mixture are non-randomly related to their traits (yields) in monoculture. Accordingly, selection is measured by a covariance function as in the Price equation of evolutionary genetics^{16–19}. The complementarity effect measures any change in the average relative yield in the mixture, whether positive (resulting from resource partitioning or facilitation) or negative (resulting from physical or chemical interference). The sum of these two effects is the net biodiversity effect; it measures the deviation of the mixture yield from its expected value on the basis of monoculture yields and the relative abundance of species in the mixtures. All three effects have the dimension of yield (where yield is a surrogate for any measurable ecosystem property), and an expected value of zero under the null hypothesis of no biodiversity effect. Consequently, all three can equally be positive or negative, and there is a potential for complementarity and selection effects to cancel each other, resulting in a zero net effect. Our additive partition unifies and relates in a single equation previous measures based on the relative yield total and proportional deviation from expected value approaches (Box 1). Another advantage over previous methods is that our additive partition provides absolute measures of biodiversity effects, thereby allowing quantitative comparison of their respective contributions.

We applied this methodology to patterns of aboveground biomass production obtained from the BIODEPTH project, a network of field experiments that examined the functioning of European grassland ecosystems in relation to the direct manipulation of plant diversity⁴. As our approach requires a comparison between the performances of species in mixture and in monoculture, we restricted its application to the subset of experimental mixture plots that contained species for which monoculture yields were available. The overall pattern for this subset was similar to that for the whole experiment⁴: a log-linear increase in aboveground biomass with species richness and a significant locality effect, but no significant interaction between species richness and locality (Fig. 1a). The net biodiversity effect was positive (the grand mean was significantly different from zero) and increased significantly with species richness beyond two species (Fig. 1b; Table 1). Species composition always had a significant effect.

The two components of this net effect, selection and complementarity, had strikingly different patterns. The selection effect

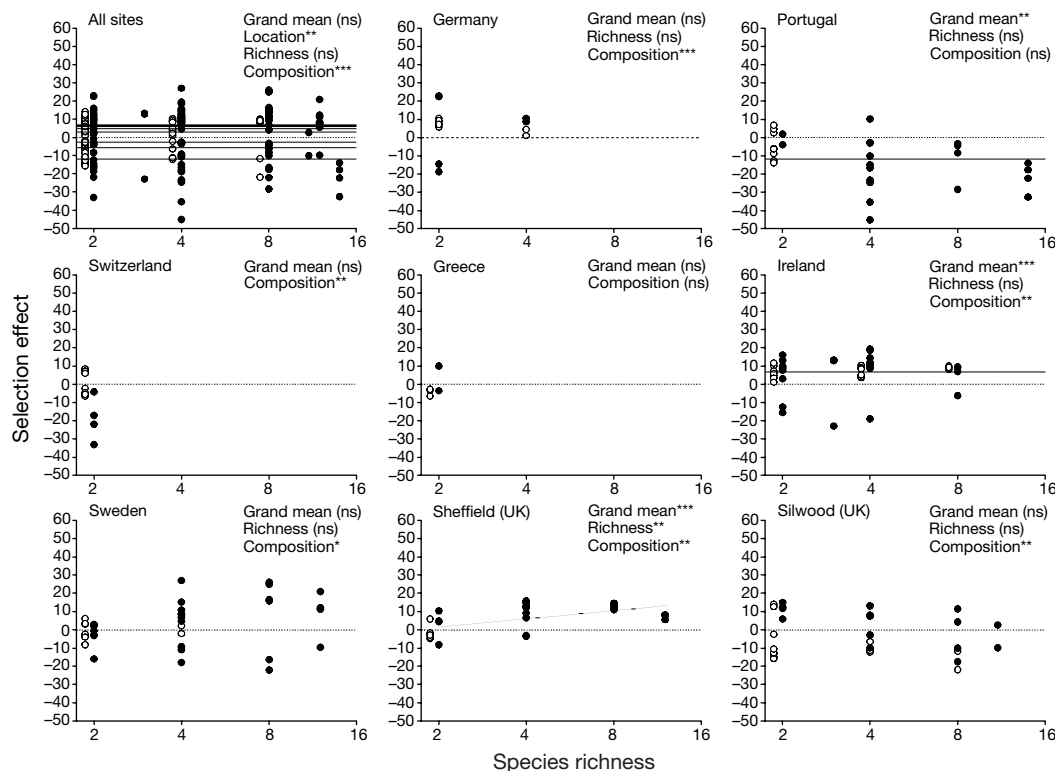


Figure 2 Selection effect, $N \text{ cov}(\Delta RY, M)$, as a function of species richness across all localities and at individual localities. Lines from highest elevation to lowest are: Ireland, Germany, Sheffield, Greece, Sweden, Silwood, Switzerland and Portugal. Values are

square-root transformed to meet the assumptions of analyses but preserve the original positive and negative signs. Symbols as in Fig. 1.

was variable, ranging from significantly positive averages in two localities (Ireland and Sheffield) to a significantly negative average in one locality (Portugal) (Fig. 2). Overall, across all sites, these variations cancelled out, so that the grand mean was not significantly different from zero, and selection was unaffected by species richness. The only factors that influenced selection significantly were locality and species composition (Fig. 2; Table 1).

In contrast, the average complementarity effect was significantly positive in four localities (Portugal, Ireland, Sheffield and Silwood) and in the overall analysis across site (Fig. 3; Table 1). Furthermore, complementarity increased significantly with the species richness of mixtures in two localities (Sheffield and Portugal) and across all localities. There were again significant locality and composition effects, but no significant locality-by-species richness interaction (Table 1). Thus, the best statistical model for the overall across-site analysis was a log-linear relationship between complementarity and species richness with identical slopes but different heights in the

various localities (Fig. 3).

One particular form of complementarity occurs between nitrogen-fixing legumes and other plants. Might the fertilization effect of legumes be sufficient to explain the positive complementarity effect found in this experiment¹¹? The presence of legumes in the mixtures did have important impacts on their performance; in general it tended to increase yields as well as the net and complementarity effects, and to generate more extreme selection effects, whether positive or negative (Figs 1–3). Although the experiment was not designed to fully separate the effects of legumes or functional-group diversity from that of species diversity, our method can also be applied to examine this issue. When the presence of legumes was included as an additional factor in our across-site analyses, species richness—in addition to locality, presence of legumes and species composition—retained a significant log-linear effect on complementarity, whether legumes were introduced after ($F_{(1,67)} = 11.36, P < 0.01$) or before ($F_{(1,67)} = 4.74, P < 0.05$)

Table 1 Summary of the analysis of biodiversity effects for mixtures of the BIODEPTH experiment

	d.f.	Net effect, ΔY			Selection effect, $N \text{ cov}(\Delta RY, M)$			Complementarity effect, $N \Delta RY M$		
		MS	F	P	MS	F	P	MS	F	P
Grand mean	1	20,000.65	129.30	2.63×10^{-18}	257.78	1.44	0.2334	15,830.07	87.74	1.87×10^{-14}
Locality	7	224.09	1.45	0.1980	1,267.88	7.09	0.0094	606.99	3.36	0.0034
Species richness (\log_2)	1	3,210.81	20.76	1.87×10^{-5}	23.35	0.13	0.7188	1,879.89	10.42	0.0018
Deviation	5	76.61	0.50	0.7789	133.54	0.75	0.5908	177.04	0.98	0.4346
Locality \times richness	5	203.89	1.32	0.2650	340.27	1.90	0.1031	110.68	0.61	0.6898
Composition	79	154.68	4.41	1.14×10^{-12}	178.79	3.13	2.59×10^{-8}	180.42	1.99	0.0005
Residual	107	35.06			57.13			90.69		
Total	205									

All terms were tested against the average variation between replicate mixtures—the Composition term—and composition effects against the overall residual (mixture-by-block interaction). The first line reports a test of the grand mean effects across all mixtures versus the null expectation of zero and subsequent lines test for effects of location and diversity. Data were square-root transformed while preserving the original positive or negative signs to meet the assumptions of analyses. d.f., degrees of freedom; MS, mean squares.

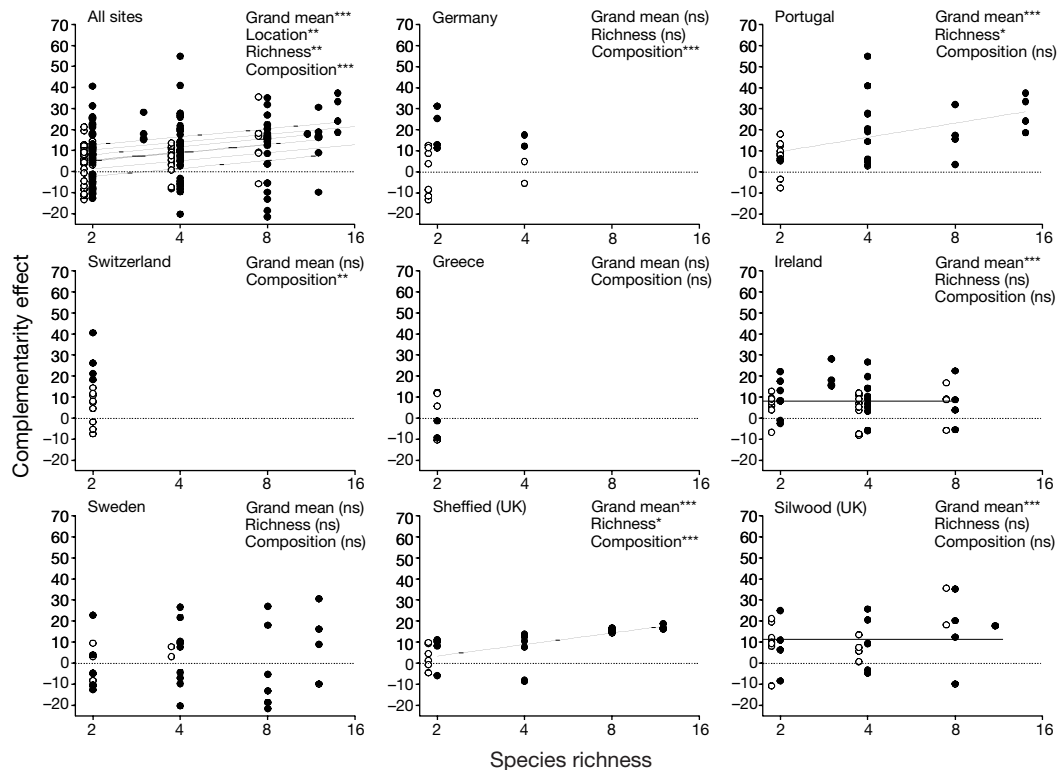


Figure 3 Complementarity effect, $N \Delta RY M$, as a function of species richness across all localities and at individual localities. Lines from highest elevation to lowest are: Portugal, Switzerland, Silwood, Germany, Sheffield, Ireland, Greece and Sweden. Values are

square-root transformed to meet the assumptions of analyses but preserve the original positive and negative signs. Symbols as in Fig. 1.

species richness. The latter test was very conservative as the presence of legumes was embedded within species richness in the experiment, so that part of the species richness effect was absorbed into the legume effect when it was fitted first in the analysis. Thus, the increased complementarity in species-rich mixtures involved not only complementarity between legumes and other plant types, but also complementarity between species within each of these groups.

Our analysis confirms theoretical predictions that selection effects should be more variable and less predictable than complementarity^{14,15}. In the BIODEPTH experiment, selection favoured species with either high or low monoculture yield depending on locality, and did not contribute to aboveground biomass patterns across localities. Therefore the selection effect can be rejected as the sole mechanism explaining the results from this experiment. In contrast, although complementarity was also variable, it was consistently positive overall and presented the same log-linear dependency on species richness as did the raw and net biodiversity effects. Furthermore, this dependence involved both complementarity between nitrogen-fixing legumes and other species, and complementarity between species within each group. Therefore, our analysis supports the hypothesis that plant diversity influences primary production in European grasslands at least partly through some combination of niche differentiation and facilitation between species⁴.

Our methodology provides a powerful means to *a posteriori* partition the selection and complementarity components of biodiversity effects in biodiversity–ecosystem functioning experiments. Our measure of complementarity, however, is linearly related to the relative yield total and, therefore, has similar strengths and limitations (Box 1). It cannot replace direct experimental investigations into the mechanisms at work in responses to biodiversity changes at the ecosystem level, which are now critical to further progress in this area. □

Methods

Experimental data

The BIODEPTH experiment simulated the loss of plant species in grassland ecosystems by removing the existing vegetation and seed bank and re-establishing plant communities from seed using standardized protocols at two localities in the UK (Sheffield and Silwood) and at single localities in Germany, Ireland, Greece, Portugal, Sweden and Switzerland. At each site, five levels of species richness were established, ranging from monocultures to higher diversity assemblages that approximately matched background levels of diversity in comparable unmanipulated semi-natural grasslands. To replicate plant diversity, each level of species richness was represented by several different plant assemblages at each site. Constrained random selection from the local pool of grassland species was used to form assemblages where all polycultures contained at least one grass. To investigate the effects of species composition, each assemblage was replicated in a minimum of two plots at each site including monocultures of many of the species involved. In total, the experiment comprised 480 plots, in which various ecosystem properties were measured. More details on the experimental design can be found elsewhere^{4,12}. For our analysis, we used data on aboveground plant biomass production measured two years after establishment of the experimental plots, in the subset of polyculture plots for which all species were also grown in monoculture at the same site. This subset comprised 205 of the 308 polyculture plots.

Statistical analyses

Data were analysed by analysis of variance and linear regression. Initial (sown) species richness was used in the analysis because it defined treatments in the experimental design; realised species richness closely matched sown species richness and produced similar results^{4,12}. Values of the selection, complementarity and net biodiversity effects were transformed to meet assumptions of tests by taking the square root while preserving the original sign (alternative transformations produced similar results). We tested two main hypotheses. First, we tested grand mean values across all polycultures versus zero to see whether they differed significantly from the weighted average of the monoculture yields. Second, we performed analysis of variance, partitioning the relationship into a linear regression, testing for positive or negative relationships with species richness above two species, and testing the deviation from this relationship. Details of similar analyses of the full set of 480 plots are available elsewhere^{4,12}.

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Cryptic evolution in a wild bird population

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Microevolution is expected to be commonplace, yet there are few thoroughly documented cases of microevolution in wild populations^{1,2}. In contrast, it is often observed that apparently heritable traits under strong and consistent directional selection fail to show the expected evolutionary response^{3,4}. One explanation proposed for this paradox is that a genetic response to selection may be masked by opposing changes in the environment^{5,6}. We used data from a 20-year study of collared

flycatchers (*Ficedula albicollis*) to explore selection on, and evolution of, a heritable trait: relative body weight at fledging ('condition'). Despite consistent positive directional selection, on both the phenotypic and the additive genetic component (breeding values, estimated from an animal model) of condition, the mean phenotypic value of this trait in the population has declined, rather than increased, over time. Here we show that, despite this decline, the mean breeding value for condition has increased over time. The mismatch between response to selection at the levels of genotype and phenotype can be explained by environmental deterioration, concealing underlying evolution. This form of cryptic evolution may be common in natural environments.

If selection acts consistently on a heritable trait in a population, it should, all else being equal, induce a permanent change in the distribution of that trait⁷. The frequent lack of expected evolutionary change in heritable traits under directional selection in the wild has therefore puzzled evolutionary biologists for some time. Explanations proposed to account for this paradox include: inflated estimates of heritability owing to environmental covariance between relatives⁷, spatially and temporally varying selection pressures⁸, negative genetic correlations between different components of fitness⁸, and selection restricted to the environmental component of the phenotype^{3,4}. Another possibility is that a genetic response to selection does in fact occur, but is masked by opposing changes in the environment^{5,6}. However, to date, these alternatives have been subjected to very little empirical scrutiny⁸.

In many passerine bird species, relative body mass (the condition index) is an important predictor of the survival of fledglings: relatively heavier nestlings are more likely to survive to become breeding adults^{9–11}. This is also true for juvenile survival in other taxa, such as reptiles¹² and mammals¹³. In the collared flycatcher, quantitative genetic analyses using traditional methods suggest a

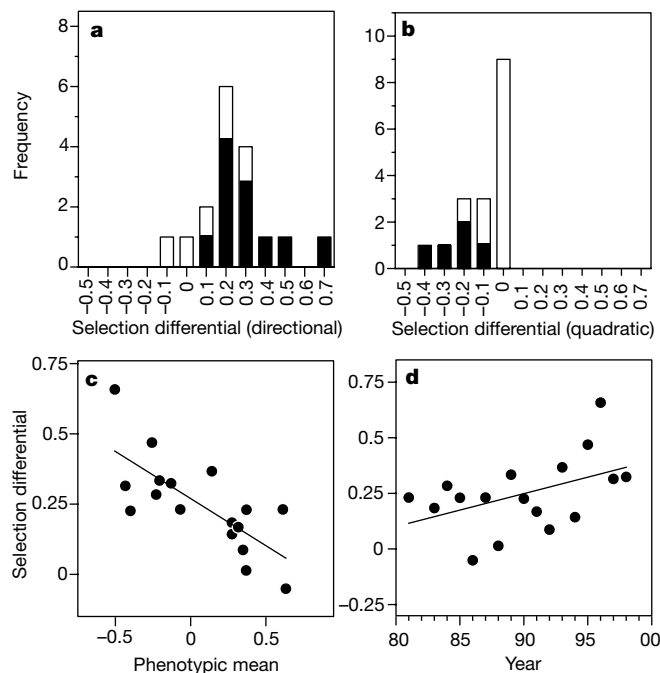


Figure 1 Patterns of natural selection on condition index of nestling collared flycatchers from 1981 to 1998. **a**, Distribution of directional standardized selection coefficients observed in each year. **b**, Distribution of quadratic standardized selection coefficients, with negative values indicating stabilizing selection. **c**, Relationship between mean condition index and intensity of directional survival selection across different study years. **d**, Intensity of directional survival selection on body condition index as a function of time. In **a** and **b**, the shaded proportions of bars indicate selection coefficients significantly ($P < 0.05$) different from zero.