INTEGRATION OF SPECIES: STASIS AND BIOGEOGRAPHY[1]

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Abstract: There are at least 11 possible causes for the integration of species in space and time; either external compulsion or internal cohesion may predominate. Both empirical and theoretical results are still ambiguous as to the prevalence of integration itself. The epiphenomenist paradigm and other relevant issues are discussed.

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When causally related or structurally similar phenomena happen to be classified into different disciplines, parallel literatures may arise or an insight in one discipline may not have occurred in the other (Cohen 1967, Van Valen 1971, Gould 1974, Ghiselin 1974). In the evolutionary half of biology this has happened several times, as in the near isomorphism of the maintenance of genic variation in a population, on the one hand, with the maintenance of a diversity of species in a community, on the other. This example arose because of the artificial separation of population genetics from ecology; the subject of the present discussion comes from the equally artificial separation of "biosystematics" from paleontology and involves a causal relation rather than an isomorphism. I ask how species-level uniformity in space and time, when it exists, is in fact maintained.

The hypothesis of punctuated equilibria (Ruzhentsev 1963, Mac Gillavry, 1968, Eldredge 1971, Eldredge and Gould 1972, Gould and Eldredge 1977, Stanley 1979) maintains, minimally, that evolution ordinarily occurs in relatively brief spurts which give rise to new species or other taxa and which are separated in time by much longer periods of near stasis. The hypothesis which may be called species integrity (see Dobzhansky [1970] for a modern treatment) maintains, minimally, that most species are geographically uniform in their most basic respects except in spatially isolated populations such as peripheral isolates or islands. The hypotheses have sporadically been related to each other, but not in a unified way. They are both aspects of species integration although it has not been established that they have similar causes.

Neither hypothesis is well established. I know of three "tests" (or frequency estimations) of punctuated equilibria in more or less random samples (Bookstein, Gingerich, and Kluge 1978, Hallam 1978, Williamson 1981); at least the first two of these studies have methodological difficulties which may perhaps affect their conclusions (too arbitrary line-fitting and inadequate geographical control and documentation, respectively). The last two studies conclude that punctuation predominates; the first concludes the reverse. The usual opinion of invertebrate paleontologists (Gould and Eldredge 1977, but see Schopf 1981 and Levinton and Simon 1980) seems to be that punctuation predominates; my subjective opinion gives the reverse for fossil mammals (cf. also Chaline and Mein 1979). This divergence of opinion agrees with the predominant result for the organisms used respectively in the three studies, but the agreement may be fortuitous because of uncontrolled geographical (Simpson 1953) and other (Gould and Eldredge 1977,

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Schopf 1981) variables.

Species integrity has never, to my knowledge, been adequately tested or its frequency estimated. An obvious difficulty it must face is the common occurrence (Stebbins 1950, Mayr 1963, Gould and Johnson 1972, Endler 1977) of appreciable geographic variation within species: clinal or stepped, concordant or discordant among characters. I discuss this under point (10) below.

Whatever their relative frequency and distribution among taxa, it is clear that both punctuation and species integrity exist and are not negligible. It is therefore appropriate to inquire into their causes, and I will discuss eleven more or less plausible mechanisms.

(1) Perhaps most evolution is neutral with respect to changes in adaptation (Kimura and Ohta 1971). Then, in various modes of gene flow, about one individual dispersing and reproducing per generation per population (irrespective of population size) suffices to override local chance effects (Wright 1931, 1969, Maruyama 1970, Crow and Kimura 1970). This value is often quoted as though it applied where stabilizing or even directional selection occurs, but it does not (Felsenstein 1976, Endler 1977). Whatever residual value this mechanism may have for species integrity, it is unimportant for punctuated equilibria. Appreciable drift is expected to occur over the one or a few million years of stasis (Lande 1976a), so some other mechanism must keep such drift from perturbing the equilibrium.

The view that the large majority of characters of the supramolecular phenotype are adaptive has recently been questioned in an influential paper (Gould and Lewontin 1979). I agree with most of the scientific aspects of this paper; indeed, I reviewed mechanisms of nonadaptive evolution (Van Valen 1960) twenty years ago, when it was much less respectable than it is now. However, I think an implication received by many readers, that evolutionary trends may commonly be nonselectively controlled and structures may commonly be nonselectively maintained, is fallacious.

Is a mouse's tail adaptive? One may examine its functions, or experiment on it. Alternatively one may note its integration of form and complex structure, and its not abnormally large variation. One may note the cost, in information as well as energy and materials, of growing and maintaining a tail. One may note that reduction of a tail is evolutionarily feasible. Such qualitative and imprecise arguments (and there are others like them) appear adequate for the conclusion that most observable evolution, and stasis, is adaptive. Indeed, such arguments were at the core of the natural theology of the eighteenth and nineteenth centuries, most extensively documented in the Bridgewater Treatises (e.g. Bell 1834).

The epiphenomenist paradigm, that apparent adaptations are reflections of others and are no more real than the shadows in Plato's cave, gains its plausibility from the view that allometric and similar relations are more or less unchangeable. If this were so, then ontogenetic allometries should normally be the same as interspecific allometries, a conclusion which is commonly false (Gould 1966, 1975, Ritland 1982). Developmental relations vary within populations (Sinnott 1958, Cock 1966, Ishchenko 1969) and evolve; most phenotypic evolution clearly involves evolution of developmental relations. Of course development imposes constraints, but adaptation can be to modify or offset such constraints as well as to ameliorate developmental side effects and adapt to the outside world. Each level and time-scale of natural selection is adaptive at that level or time-scale, but connections of function among levels may be tenuous or even reversed, and so we may look at a real adaptation but think it is nonadaptive or even inadaptive merely because our scale is wrong.

(2) Perhaps gene flow overrides locally adaptive selection (Mayr 1963, Hebert 1979, Stanley 1979, Jackson and Pounds 1979). Two related sorts of evidence

support this mechanism for species integrity, although again it is inapplicable over geologic time. Populations on islands, or otherwise peripherally isolated from the main body of the species for along enough time, commonly diverge much more than would be expected from their geographical position with respect to the main body of the species (Mayr 1942, 1963). Moreover, rodents seem to have adapted in color to unusually colored backgrounds mostly in situations where they have little opportunity for gene flow with their normally colored relatives (Benson 1933, Hooper 1941, Mayr 1963). This even seems to be the case (Bowen 1968) in the coloration of Peromyscus polionotus, which Haldane (1948) had used in his classic analysis of a cline.

However, gene flow in most species is much too low to override divergent selection in distant populations (Durden 1969, Ehrlich and Raven 1969, Mayr 1970, Levin and Kerster 1974, Levin 1979, 1981), despite occasional long-distance dispersal and the leptokurtic shape of dispersal, which produces relatively long tails to the distribution. Indeed, it would be useful to have even an order-of-magnitude estimate as to how frequently sympatric populations of different species of one kind or another exchange genes more than do distant populations of the same species (Levin and Kerster 1974, Van Valen 1976). Islands have special adaptive conditions of their own, especially biotically, and the rodent cases may be due to swamping of small populations by much larger neighboring populations, a phenomenon which is obviously inapplicable generally. (A very large Mexican lava flow has locally adapted rodents despite gene flow from outside [Baker 1960].) Both kinds of cases, however, deserve restudy from modern viewpoints.

A superficially similar phenomenon occurs where there is a single generally adapted phenotype for a region. If local extinction-recolonization cycles are frequent, local populations may diverge nonadaptively. Dispersal can re-introduce the regionally optimal phenotype, which gives greater geographic uniformity than is the case without dispersal. Lokki et al. (1976; Saura et al. 1977) found an apparent example of this in obligately parthenogenetic insects. Little dispersal is needed to infect a population with an adaptively superior genotype, while very much more is needed to counteract locally adaptive differentiation.

A recent study (Slatkin 1982) uses a new method to estimate gene flow and produces estimates of both high and low rates of gene flow among natural populations of various real animals. However, this method has at least one theoretical problem if there is selection and lacks adequate documentation of the results. High gene flow will be estimated as low if there is selection for different alleles in different populations, thereby making alleles present in a few populations relatively numerous. An empirical problem with this method comes from the only case I know where it can be compared to real data. Results about to be published from Lewontin's laboratory suggest an effective population size N of 10^4 or 10^5 for two populations of Drosophila pseudoobscura. This agrees with the very imprecise value estimated by Wright, Dobzhansky, and Hovanitz (1942). Comparison of Slatkin's Figures 2 and 3 suggest that the product Nm should be more than 1, where m is the rate of gene flow between populations sampled. Thus m should be more than 10^{-5} in this case, which I think is unreasonable (Dobzhansky 1974; Dobzhansky and Powell 1974). m is the probability of reproductively successful dispersal per individual per generation from one population to the next. In the data Slatkin used the "next" population was usually hundreds of kilometers away. Alternatively, the product Nm can be considered as a unit, with the resulting expectation of one fly per population moving hundreds of kilometers every generation to land in the right area each time. It remains possible, however, that additional work can resolve the apparent discrepancy, and at the least the approach is potentially important.

(3) Perhaps gene flow is too low to carry favorable alleles between distant populations (Stanley 1979). This mechanism would oppose species integrity and

promote stasis if it would work, but it does not work (Felsenstein 1976). Again there seems to be a confusion between movement of neutral and advantageous alleles. Moreover, for ordinary polygenic quantitative characters a mutation rate of roughly 10^{-3} or 10^{-2} per individual per generation can be expected (Lande 1976b), so variation continually arises throughout the species.

(4) Perhaps many populations are too large for evolution to occur at an appreciable rate (Stanley 1979, Gould 1981). This view rests on a misinterpretation of part of Wright's shifting-balance theory of evolution, where genetic drift in small effective populations permits shifts from local optima to higher adaptive peaks. (Environmental variation on a time-scale to which selection can respond produces the same effect and I suspect is more important.) In fact it is large effective populations, not small ones, which are most responsive to overall natural selection within populations (Fisher 1930), merely because effects of drift and very local selection are minimized; this does not disagree with Wright, although Wright's emphasis differed.

(5) Perhaps there is inadequate genetic variance for differentiation (Selander et al. 1970). That this is ordinarily false empirically, by now needs no discussion (Mayr 1963, Lewontin 1974).

(6) Perhaps the adaptive circumstances are unique in each population and therefore little evolution occurs (Herbert 1978). In part this is an extreme case of mechanism (1), but it can also operate if local populations are ephemeral. The distribution of population lifetimes, for various kinds of species, remains a major unsolved problem of ecology. Because some geographic variation in phenotype occurs (Mayr 1963) in almost all adequately studied species (therefore why not more if each population is really unique?) and because the mechanism does not apply over geologic time, we should try to find something better. This conclusion is strengthened by the prevalence of adaptations useful throughout a species' range. Presumably most adaptations are at least this general. See also (10).

(7) Perhaps the developmental system of a species is ordinarily difficult to change without disrupting it (Mayr 1963, Eldredge and Gould 1972, Frazzetta 1975, Gould 1980). This mechanism is the first which applies to both manifestations of the integration of species. That closely related species commonly have more or less incompatible controls on development is shown by the standard observation of inviability or sterility in species hybrids. Yet it is often absent; many hybrids, especially but by no means only among plants, are more or less fully fit (Anderson 1949, Mayr 1963, Grant 1981), and reproductive isolation (or at least the continued coexistence of sympatric species: Carson 1975, Van Valen 1976) is then caused in other ways. Moreover, the prevalence (Ehrman 1962, Dobzhansky and Powell 1975b, Grant 1981) of reported cases of weak or partial developmental incompatibility requires that we be cautious in ascribing a rapid origin to most fully developed cases. How often have we simply missed a slow transition?

In the fossil record transitions among species would be expected by this hypothesis to consist of populations more variable than would species in stasis, because of low developmental integration. Such a pattern has been documented for ostracodes (Sylvester-Bradley 1976) and molluscs (Williamson 1981), with isolated cases reported by other authors both supporting and not supporting the prediction. However, the same pattern is expected if adaptive zones (niches) change during or near speciation (Van Valen 1969, Stitt 1971), as they commonly do and necessarily do if species are distinguished, in principle, ecologically (Van Valen 1976). Pre-existing stabilizing selection would be relaxed in one or more directions, so permitting wider variation. Williamson (1981) lumped both ancestral and derived species in his analysis when they coexisted (P.G. Williamson, personal communication, 1981) thus explaining the otherwise anomalous position of the sample of Bellamya unicolor at level 28 but thereby possibly introducing an artifact into his analysis of variation by increasing the variation measured.

High variation can occur not merely in the transition from one species to
another, but also in the transition between adjacent subspecies (Mayr 1963, Corbin
1981). It can be associated with primary as well as secondary intergradation
(Endler 1977). Indeed, stepped clines ("area effects") with no apparently
associated stepped environmental variables occur in a number of species (Endler
1977), although perhaps rather rarely overall, and in one case the step even shifted
position more rapidly than the dispersal capability of the species (Creed et al.
1970). High variation may also be associated with rapid evolution (Fisher 1930,
Guthrie 1965), especially in depauperate adaptive zones (Simpson 1953, Van Valen
1969, Stitt 1971, Ford 1975, Waldron, Hilton, and Ambrose 1976), and can have
various other causes.

(8) Many characters of many organisms are more or less canalized (Waddington
1957, Rendel 1962, 1967), which means that variation in environmental and genic
influences has little phenotypic expression within some range of these influences.
Perhaps such canalization prevents significant phenotypic expression of evolution
from occurring until a boundary of the canalization is passed (Hoffman 1981). The
phenotype could then change rapidly.

This mechanism differs from (7) in two ways. First, it causes no internal
resistance to evolutionary changes, merely an inhibition on their expression in
some aspects of the phenotype. Secondly, the degree of canalization differs for
different characters, and moreover the specific developmental processes producing
canalization usually differ among characters (Van Valen 1962, Soulé 1967, Mason,
Ehrlich, and Emmel 1967, Soulé and Baker 1968, Rapport 1973). Thus, if a breakdown
of the canalization is not to occur by accumulation of genic variations produced
randomly or as byproducts of other selection, a diversity of selection pressures
must be maintained. The problem of genetic and phenotypic load, of there not being
enough variation in fitness to produce a set of apparent responses, is relevant here
and remains a significant and general empirical problem.

It is important to distinguish between the process of selection and the
response to it. This seems to be forgotten by nonspecialists every few years.
Heritability, e.g., is irrelevant to the process but necessary for a response,
although its existence can ordinarily be assumed from the almost universal success
of artificial selection experiments. The great amount of effort being spent just
to show that interesting characters are heritable is therefore probably a mistaken
emphasis in most cases. Stabilizing selection may result in a developmental response
of canalization, but it may alternatively result in a mere reduction or removal of
alleles and combinations which tend to extreme phenotypes, a "normalizing" response.

Evolution away from a zone of canalization produces higher phenotypic
variation, as do the other processes discussed in (7). However, the zone of
canalization itself is evolutionarily labile and can change position in response to
selection (Fraser et al. 1965, Rendel 1979). For this reason, and because of the
need for recurrent selective maintenance of canalization, it seems inadequate as a
cause of species integration although is may be part of the response.

(9) Perhaps the genome of a population is sufficiently coadapted that relatively
small changes tend to disrupt it; coadapted genotypes in Wright's phase space of
possible genotypes are then usually separated be adaptive valleys (Mayr 1963, 1975,
Ehrlich and Raven 1969, Dobzhansky 1970, Carson 1975). Formally this mechanism is
about the same as (7), because genes express themselves developmentally. However, the
emphasis differs appreciably. Lerner (1954) called this process genetic homeostasis.
(This term is often confused with developmental homeostasis, the buffering of
development against environmental or genic variation, which is the same as canalization.)
Genetic homeostasis occurs when alleles or phenotypes tend to return to their initial
frequencies when their frequencies are changed. Thus response to a new selective
pressure commonly reduces an organism's fitness with respect to its initial environment
and with respect to the initial epistatic interactions; if the new selection is relaxed
soon enough, the population may still be able to return to the vicinity of its initial
genotypic adaptive peak (Wright 1980). Other causes are possible; Lerner (1964)
emphasized heterosis.

A related phenomenon involves an often large increase in both chromosomal and genic mutation rate when crosses are made between different populations. This is best known in Drosophila (Thompson and Woodruff 1978, 1980; Woodruff et al. 1979; Bregliano et al. 1980) but is probably more general (Thompson and Woodruff 1978). The mutations are effects of transposable elements (Spradling and Rubin 1982), but the normal inactivity of the presumptive mutators occurring within a given population implies selection against such activity (Thompson and Woodruff 1978). This is an aspect of a coadapted genome. Another aspect is the decrease in fitness commonly seen (Vetukhiv 1953, 1954, 1956, Vetukhiv and Beardmore 1959, Brncic 1954, 1961, Dobzhansky and Powell 1975a, b) in the F_2 generation (but usually not the F_1) of crosses between different populations. Other sorts of disruptions may also occur in such crosses (Barton and Hewitt 1981), although the well-studied case of Rana pipiens (Moore 1957) has proved to involve different species or semispecies (Pace 1974), some of them long known but improperly rejected.

We see that much of the evidence for coadapted genomes comes from differences within species with respect to coadaptation. Integration in this way at the species level is shown by the very existence of postmating reproductive isolating mechanisms, and it may well be (White 1978) that chromosomal-level causes of such isolation are especially likely to occur during speciation itself. The relation of such kinds of coadaptation to restriction on morphological and adaptive change, however, is not at all clear. Artificial selection experiments almost always give an appreciable response, although with an associated decline in fitness. And what seems to have been a coadapted change in Drosophila population genomes over a wide area has actually been observed in nature (Golubovskii et al. 1974).

A coadapted genome need not imply much realized epistatic interaction, because non-coadapting alleles would be more or less eliminated during the evolution of coadaptation. Thus the usual observation (Langley, Smith, and Johnson 1978) of approximate linkage disequilibrium among isozyme loci does not argue against prevalent coadaptation. Less importantly, isozyme assays ordinarily detect structural genes, and it would be surprising if these were important in coadaptation. Nevertheless there is a considerable body of evidence on the importance and prevalence of epistasis (Dobzhansky 1970, Ford 1975, Endler 1977, Hartl 1977a, b, Hedrick, Jain and Holden 1978, Wallace 1981), and interactions of otherwise normal alleles at different loci can even produce lethality or sterility (Dobzhansky 1970).

It is with respect to a coadapted population genome that the cohesive effect of gene flow gains some plausibility. An occasional immigrant from a population differently coadapted would be selected against in the same way that postmating reproductive isolation operates. However, a persistent influx of such immigrants, if numerous enough, would themselves exert a selective pressure on the local population for alleles and allelic combinations that are not specially coadapted, that are "good mixers" in Mayr's phrase (1954). Quantitative estimates of how much gene flow is needed will obviously vary strongly, depending on the the specific nature and strength of the coadaptation. Although this mechanism can empirically be negligible (Creed et al. 1970), stepping-stone gene flow may nevertheless in principle inhibit the evolution of locally coadapted genomes (Echelle, Echelle, and Taber 1976, Bouchet 1981, Curry and Hughes 1982). Of course gene flow is irrelevant to stasis, as distinct from species integrity.

(10) Possibly stabilizing natural selection is sufficiently uniform on a given species (Hoffman 1978, Lande 1980, Stebbins and Ayala 1981, Charlesworth, Lande, and Slatkin 1982) that it maintains its phenotype relatively constant over long geographic distances and over geologic time. This general possibility is less absurd than it may seem. It seems absurd because it does not seem helpful (Tabin 1981). Why stasis? Patterns should have explanations that make us understand why there are these particular patterns. Species commonly exist in rather diverse

environments, and commonly adapt to the differences in these environments. Why
should they not change as their biotic and physical environments change?

However, observations do not exclude the possibility that such local
adaptation is usually rather superficial, that the more important aspects of the
species' niche remain more or less constant in their frequency distribution. If
so, stabilizing selection in itself can account for the integration of species.
The mechanism here is external compulsion rather than internal compulsion.

There is not a sharp demarcation between compulsion and cohesion. Genetic
homeostasis functions to inhibit response to temporary environmental changes; too
close tracking of a fluctuating environment can be deleterious (Levins 1968).
Nevertheless, developmental integration and coadapted genomes do often change
within single species, as noted above for geographic differentiation, but the
visible phenotype remains little changed. Sib species, which isozyme analyses
tell us are probably much more numerous than realized before, extend the effects
of stabilizing selection beyond the species level. Asexually reproducing species,
from the other direction, tend to maintain unity without any interchange of genes.
They often have less discrete boundaries than do sexual species (Stebbins 1950,
Van Valen 1964, 1976, Hutchinson 1968, Gordon 1978, Grant 1981), but the existence
of modality itself is relevant. Indeed, considerable evolution can take place
without sexual reproduction (i.e., gene exchange), as shown by the lack of discovery
of males in the entire order (or class) Bdelloidea of rotifers (Hutchinson 1968).

Angiosperm families are commonly characterized by reproductive adaptations
(Stebbins 1970, 1971, 1974) which remain more or less constant while a family may
diversify exuberantly in other more obvious ways. This pattern is a matter of
phylogeny rather than of an arbitrary definition of families. The stabilizing-
selection hypothesis for species integration is analogous but at the level of species
rather than the family. The well-known difficulty of distinguishing such essential
characters, if they do exist, from more easily modifiable characters, was a major
factor in the reaction against typological systematics (Simpson 1961, Hull 1965,
Mayr 1969). However, such difficulties in detection have no bearing on whether
there really is such a difference. Species integration almost implies the existence
of essential characters of some kind, whether maintained by developmental cohesion
or selective compulsion. Unlike the older view, such characters may vary under
unusual circumstances.

Most of the presumptive speciation events Williamson (1981) observed were at
times of easily detectable physical stress to lake molluscs, by a major lowering of
the lake level, a major volcanic eruption that produced a large ashfall onto the lake,
or both. Indeed, all observed lineages speciated almost simultaneously at one of
the stresses. Among them is Melanoides tuberculata, now an obligatorily parthenogenetic
species. The overall similarity of its pattern of speciation to that of the several
sexual lineages may seem to be inconsistent with cohesion being responsible for its
times of stasis. If cohesion kept it from speciating during unstressful times, why
should it not also prevent this during stress? To say that more deviant phenotypes
are ordinarily less well adapted, or to invoke a change in adaptive zone under
stressful conditions, seems to explain the stasis by uniformity of stabilizing
selection. This conclusion is clearest for M. tuberculata, but it probably applies
in the same way to the sexual species. However, an explanation by cohesion would
maintain stasis despite minor fluctuations in the adaptive zone; phenodeviants are
unconditionally deleterious until the adaptive peak shifts far enough away to make
the cohesive development itself deleterious (cf. Wright 1980). A threshold effect
results, one for which cohesion is necessary.

Purely adaptive thesholds exist also and may be common (Levins 1968, Endler
1977). A structure can be used for more than one function, for which there are
different optimal states of the character. If the fitness set is concave
(intermediate character states are worse than either pure adaptation), selection will

and temporally constant. Only the latter would then exhibit integration. However, even such a classification has some, perhaps many, exceptions. One interesting kind of exception is provided by Drosophila subobscura, which is geographically much more constant (Götz 1965, Pinsker and Sperlich 1979, Sperlich et al. 1981) than is its relative D. pseudoobscura (although both are uniform morphologically) but lacks evidence for coadaptation (McFarquhar and Robertson 1963, Sperlich and Feuerbach-Mravlag 1974). Indeed, Carson (1975) and Mayr (1973) have proposed that part of the genome of at least some species is internally coadapted and part is not, although this proposal remains hypothetical.

Because of the lack of coincidence in some cases (perhaps even usually) of the several kinds of differences observed among species, it is impossible to assert that a revolutionary reorganization of the genome must accompany speciation. Thus there is no theoretical justification for the view that punctuation is necessary. [A minor theoretical justification (Gould 1982), that selection among species (Lyell 1832) or lineages (Simpson 1953, Van Valen 1975) would be impossible with gradual change, is an error of categories (cf. Slatkin 1981). Species have fuzzy boundaries whether punctuated or not, and in fact I discovered (Van Valen 1964) what were later (Zadeh 1965) called fuzzy sets because species are anomalous in classical set theory. Nothing prevents a set, fuzzy or sharp, from acting also as an entity itself (Van Valen 1977).]

Whether species integrity, when it occurs, is caused in the same way as stasis, when this occurs, remains to be determined, although the similarity of the phenomena does suggest a similar cause.   Like punctuation and gradualism themselves, both compulsion and cohesion seem sometimes to be important but estimation of their relative predominance does not seem feasible by existing methods.

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