Evolvability, Dispositions, and Intrinsicality

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In this paper I examine a dispositional property that has been receiving increased attention in biology, *evolvability*. First, I identify three compatible but distinct investigative approaches, distinguish two interpretations of evolvability, and treat the difference between dispositions of individuals versus populations. Second, I explore the relevance of philosophical distinctions about dispositions for evolvability, isolating the assumption that dispositions are intrinsically located. I conclude that some instances of evolvability cannot be understood as purely intrinsic to populations and suggest alternative strategies for resolving this difficulty.

1. Introduction. Dispositional properties have been an ongoing interest for philosophers of science because of their persistent use in the explanatory discourse of science. Within the biological sciences, the concept of fitness has received the most attention because of its centrality in contemporary evolutionary theory and the worry that it was inherently tautological. To this end, effort has primarily been expended on whether or not fitness *is* a dispositional property rather than specifying what *kind* of dispositional property it is. This difference is not idle because some dissent from characterizing fitness as a propensity arises from skepticism about the philosophical status of dispositions (Rosenberg 1984).

The aim of this paper is to explore a different dispositional property in biology, "evolvability" (the capacity to evolve), by viewing how philosophical characterizations of dispositions correspond to current scientific

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usage. Assuming evolvability *is* a dispositional property, what kind of disposition is it? This strategy is promising for several reasons. First, evolvability is not currently taken to be central to evolutionary theory and thus there is less reason to argue about the nature of evolutionary theory itself—a vigorous part of the fitness debate. Second, evolvability has become increasingly prominent over the past decade, especially in the emerging discipline of evolutionary developmental biology. "[E]volutionary developmental biology (EvoDevo) expects to articulate how the diversity of organic form results from adaptive variation in development. . . . [T]he central problem of EvoDevo is to understand how the architecture of development confers evolvability" (Von Dassow and Munro 1999, 307). Third, an exploration of a different dispositional property affords the opportunity to reexamine assumptions within a philosophical literature that has largely been forged on fragility and solubility.

My analysis consists of two main components. First I attempt to characterize evolvability from recent literature. I identify three compatible but distinct investigative approaches (computational, theoretical, and empirical), distinguish a universal and restricted interpretation of evolvability, and treat the difference between dispositions of individuals versus populations. The second component explores philosophical distinctions about dispositions, such as the assumption that dispositions are intrinsically located, in order to understand evolvability. I conclude that some instances of evolvability are not purely intrinsic to populations and suggest alternative strategies for resolving this difficulty.

2. Characterizing Evolvability.

2.1. Approaches. Three distinct approaches to evolvability can be discerned in recent literature. The first is a *computational* strategy that arises out of genetic algorithms in computer science. Evolvability is not distinctly biological but rather is abstractly characterized as, "the ability of the genetic operator/representation scheme to produce offspring that are fitter than their parents" (Altenberg 1994, 47). Closely allied to computational strategies are *theoretical* approaches, which can be distinguished further from *empirical* ones. The distinction between computational and theoretical captures the fact that computational approaches to evolvability need not concern biological entities and that theoretical approaches are intentionally biological in orientation but need not have a computational component. The line between theoretical and empirical is a continuum that does not preclude their joint consideration. The basis of this continuum is the degree of substrate neutrality claimed for the account of evolvability. In other words, are there any restrictions on the entities that can have this capacity to evolve? Theoretical approaches adduce analyses of evolvability

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that are broadly applicable to biological entities (''substrate neutral'') while empirical approaches often start from the observation of evolvability in a concrete system (''substrate biased''). A natural affinity exists between computational and abstract theoretical approaches since in the former the entity is nonbiological (computer program segments), which makes substrate neutral accounts more relevant (cf. Altenberg 1994). These three strategies are discernibly different but not mutually exclusive.

In an early theoretical approach with a computational component, Dawkins argued that evolvability requires entities capable of self-replication and a developmental process where these replicators influence a phenotypic outcome (Dawkins 1989). These conditions revealed the need for a constrained ontogenetic process when instantiated in a computer simulation. Evolvability is due to an embryology that generates a more fruitful gamut of phenotypic variation within particular constraints. Sterelny developed a noncomputational account inspired by Dawkins, but with an explicit attempt to expand the class of replicators beyond genes (Sterelny 2001). Isolating the importance of heritability for evolutionary processes, he details general specifications for an inheritance mechanism such as allowing for cooperation through division of labor and the ability to generate a wide range of variation. Along with further subspecifications, these provide criteria for evolutionary potency or evolvability (2001, 338–342). Wagner and Altenberg offer a blended theoretical/computational account that utilizes the concept of a *genotype-phenotype map* (Wagner and Altenberg 1996). They focus on abstract principles of variability that would need to be true of a genetic system generating variation. One can articulate a theory about selection acting on properties of a genetic system that lead to particular properties of the genotype-phenotype map that are more evolvable.

Two observations are in order. First, these approaches do not focus on the ''environment'' in which a system meeting the above criteria would be found.[1] Evolvability is an intrinsic property of a biological system, evidenced by a focus on genetic properties, assuming necessary but unspecified external conditions. Second, ontogeny is crucial, whether in Dawkins's constrained embryology or the physical constituents of the genotype-phenotype map. Two of Sterelny's subspecifications for the generation of variation are constraints on the kind of developmental processes required for the capacity to evolve.

Other theoretical approaches exist, but it is more useful to survey empirical studies of evolvability. Biological phenomena that have been discussed in relation to evolvability include fluctuating asymmetry (Van

1. Sterelny explicitly recognizes this and it is implicit in Wagner and Altenberg's fitness function.

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Dongen and Lens 2000), heat shock proteins (Rutherford and Lindquist 1998), developmental modularity in holometabolous insects (Yang 2001), mutation rates and mutator alleles (Burch and Chao 2000; Radman, Matic, and Taddei 1999), and yeast prions (True and Lindquist 2000). In the latter case, a prion serves as a protein-based element of inheritance in *S. cerevisiae* by facilitating novel phenotypic variation through the suppression of normal translation termination sites during protein synthesis (Li and Lindquist 2000; True and Lindquist 2000). The prion, when present and active, confers the ability to generate more heritable phenotypic variation, especially when yeast colonies are subjected to variable growth conditions, providing a selective advantage to prion possessors. Thus, prion possession likely confers selectable benefits in fluctuating or erratic environments (True and Lindquist 2000). The significance of an empirical approach is the ability to identify evolvability in existing populations, thereby substantiating its evolutionary significance via experimental systems.

Consonant with the observation that ontogeny plays a critical role in theoretical accounts of evolvability is its prominence in the nascent discipline of EvoDevo, observable in the work of Gerhart and Kirschner (Gerhart and Kirschner 1997, ch. 11; Kirschner and Gerhart 1998). They argue that there are four distinguishable aspects of biological systems that can confer evolvability or the capacity of a lineage to generate heritable, selectable phenotypic variation: versatile protein elements, weak linkage, compartmentation, and exploratory behavior. For example, exploratory behavior refers to a system's epigenetic mechanisms for exploring the space of variation during and after ontogeny such as in microtubule skeletal morphogenesis. Compartmentation, or *modularity* (Winther 2001), "reduces the interdependence of processes, consequently reducing the chance of pleiotropic damage by mutation and increasing phenotypic variation" (Kirschner and Gerhart 1998, 8423). If organisms are composed of spatiotemporal modules at multiple hierarchical levels, then dissociation among modules during ontogeny can produce more degrees of freedom in generating phenotypic variation via duplication, divergence, and co-option (Raff 1996, 325ff). These four aspects confer evolvability by providing flexibility and robustness in biological processes. They "deconstrain" the stringent requirements of functional integrity that would prevent or hinder evolutionary change.

2.2. Evolvability$_U$ / Evolvability$_R$ and Intrinsic Capacities of Groups. All lineages technically have some capacity to evolve, i.e., the ability to descend with modification is universal. I designate this as evolvability$_U$. In quantitative genetics, evolvability$_U$ is understood as "the ability of a population to respond to natural selection," which is formalized into a trait's heritability multiplied by the square root of its additive genetic variance,

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divided by the population mean of the trait (Houle 1992, 195–197). This notion is operationally useful for the study of natural selection in extant populations but less directly applicable across geological time. Difficulties of deriving historical results are explicit in the formal framework since evolvabilities under different selection regimes are not informatively comparable (1992, 202).

The recent attention paid to evolvability is due to a restricted definition intended to explain differential evolutionary success, which I label evolvability$_R$ (cf. Brookfield 2001). Although the distinction between evolvability$_U$ and evolvability$_R$ is one of degree, the distinction highlights a different explanatory aim: whether or not specific systems or organizational structures confer evolvability$_R$ over and above evolvability$_U$. Isolating the property structure of evolvability$_R$ will potentially shed light on branching events and the proliferation or extinction of different organismal lineages in evolutionary history. "The use of Hsp90 as a capacitor for the conditional release of stores of hidden morphogenic variation may have been adaptive for particular lineages, perhaps allowing the rapid morphological radiations that are found in the fossil record" (Rutherford and Lindquist 1998, 341). If evolvability$_R$ contributes to "developmental depth" or "evolutionary versatility" then it might account for apparent large-scale trends in evolution (McShea 1998). "Information about [origination, persistence, and extinction probabilities] is desirable, because they might reflect something fundamental, something inherent to the supertaxa of organisms themselves . . . their intrinsic capacities for diversity change" (Gilinsky and Good 1991, 161). The question is whether this intrinsic capacity is the disposition of evolvability$_R$.

In order for evolvability$_R$ to explain differential success in contemporary evolutionary theory, the disposition can only be ascribed to populations (or lineages), not individual organisms. Individuals do not evolve and thus cannot have the capacity to evolve. Fitness, by way of contrast, can be understood as a dispositional property of individuals *and* populations. If we define a group as "a set of individuals that influence each other's fitness with respect to a certain trait but not the fitness of those outside the group" (Sober and Wilson 1998, 92), then evolvability can be considered a population-level trait that exclusively influences the fitness of population members. But because evolvability is a disposition, and thus not always manifested, it is a trait very different than limb length. Consider a recent definition:

> The evolvability of an organism is its intrinsic capacity for evolutionary change . . . it is a function of the range of phenotypic variation the genetic and developmental architecture of the organism can generate, and thus the amount of variation available on which selection can act. (Yang 2001, 59; cf. Radman, Matic, and Taddei 1999, 146)

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Reading "organism" as organism *kind,* the trait under consideration is the "genetic and developmental architecture" and the population-level manifestation of this disposition is a "range of phenotypic variation." Returning to evolvability in EvoDevo, we can single out modularity as a more specific aspect of the genetic and developmental architecture. Modularity contributes to the manifestation of evolvability by reducing functional interconnection between modules, which allows for a greater range of variation through duplication, divergence, and co-option of individual modules. As environmental regimes change, a population that demonstrates a greater range of viable phenotypic variation is likely to yield more branching lineages than a population that generates a smaller range of variation, and thereby the former is more evolvable than the latter *(ceteris paribus)*.

What does it mean for the disposition of evolvability to be *intrinsic*? Modularity is intuitively intrinsic to a particular organism but what is it to be *intrinsic to a population*? The criterion of spatial location (inside or outside) is deceptive because population structures may not be spatially cohesive. Evolvability may often be construed as intrinsic precisely because it is connected with properties of the genetic and developmental architecture of individual organisms. In elucidating the cognate notion of "adaptability," Endler isolates its distinctness in terms of its relation to many environments rather than one particular environment (Endler 1986, 48). But we cannot construe intrinsicality without respect to *any* environment since this is biologically implausible. Middle ground could be available in taking the intrinsic/extrinsic distinction to be one of degree. Brandon adopts this approach in his criticism of Michod's attribution of intrinsic properties to genotypes (Brandon 1990, 27–39). We might link intrinsicality with effects on population-level fitness, connecting Sober and Wilson's definition of a group with the location of factors affecting one group's fitness rather than another with respect to the trait of evolvability$_R$. Although appealing, it raises the specter that intuitively extrinsic factors that significantly contribute to fitness differences between groups may become included in the supposedly intrinsic disposition to evolve.

3. Philosophical Distinctions. We are now in a position to turn to philosophical treatments of dispositions that may be applicable to evolvability. A variety of distinctions about dispositional properties currently exist (cf. Mellor 2000). Although we cannot discern the bearing of every distinction for evolvability here, refinement in the philosophical literature on dispositions allows us to be selective. It is worthwhile to keep a general but contentiously vague definition at hand; "a disposition is a property (such as *solubility, fragility, elasticity*) whose instantiation entails that the thing that has the property would change, or bring about some change, under certain conditions" (Crane 1996, 1). One basic distinction is whether dispositions

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are probabilistic or deterministic (Mackie [1977] 1978). A deterministic disposition is always manifested under appropriate stimulus conditions while a probabilistic disposition may or may not manifest even when stimulus conditions are fulfilled. Evolvability is a probabilistic disposition because a lineage may not evolve even when it has the capacity to do so; its manifestation is a function of stochastic processes in populations. Because evolvability is a disposition of populations rather than individuals, it inherits this aspect of the population level processes.

3.1. Intrinsicality. Almost every discussion of dispositions acknowledges that they can be couched in terms of one or more subjunctive conditionals. A common starting point has been a "simple conditional analysis":

> [A]n object or entity x is disposed at time t to give response r to stimulus s iff, if x were to undergo s at t, x would r. (Lewis 1997, 143)

The inability of this or a minor variant to adequately handle ascriptions of dispositions is revealed by attending to the persistence conditions of a disposition (Martin 1994). If a disposition can be gained or lost in the process of manifestation, the conditional analysis is flawed. These *transient* dispositions have traditionally been masked via implicit *ceteris paribus* clauses that rule out the possibility of dispositions being acquired or lost. Attempts to circumvent the problem via "reformed conditional analyses" yield a sharper line between the intrinsic properties of an entity and its surrounding environment by modifying the biconditional; "for some intrinsic property B that x has at t, for some time t' after t, if x were to undergo stimulus s at time t . . ." (Lewis 1997, 157). Although still controversial (Bird 1998), these analyses highlight landmarks to explore with respect to evolvability. Is evolvability an intrinsic property? Is it transient?

Clearly evolvability$_U$ is not transient since it is always present according to current evolutionary theory. But evolvability$_R$ must be either gained or lost in some instances in order for it to be a measure of the differential success of clades in the history of life. A lineage can acquire or lose the components identified by Gerhart and Kirschner and succeed or fail evolutionarily as a result. Now the question involves scrutinizing what exactly accounts for the transitory nature of evolvability$_R$, which can be reframed as a query about the *causal base* of the disposition. Gerhart and Kirschner identified four elements that can compose a property complex to confer the disposition of evolvability: modularity, versatile protein elements, weak linkage, and exploratory behavior. The contribution of these elements is variable and none are individually necessary or jointly sufficient for evolvability$_R$ to obtain in a population. The transience of evolvability does not coincide with the presence or absence of particular properties in

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the causal base (cf. Lewis 1997, 150).[2] Rather, it is explicated in terms of the coming and going of these various properties in conjunction with observations of the success and failure of clades.

The focus on ontogenetic processes highlighted above allows for an easy slide from intrinsic for an *individual* to intrinsic for a *population* (or group). Intrinsic properties in a particular organism's ontogeny such as modularity can be extended to understand the manifestation of the disposition at the level of phenotypic variation in a population. But if we attempt a more formal explication of group intrinsicality by linking it with fitness effects, then extrinsic properties may become relevant to the capacity of a population to evolve. Weber noted this worry in a discussion of fitness, highlighting that a reduction of organismal fitness to various intrinsic physical properties might not be possible because fitness is always a function of a specific environment composed of many abiotic and biotic factors (Weber 1996, 428–429). Although evolvability$_R$ is not defined in relation to a particular environment, it cannot be intrinsic in the sense of environmentally invariant. If evolvability$_R$ must be relativized to some set of environments, it will be difficult to understand it as purely intrinsic to a population (cf. Brandon 1990, 37–39). This concern also arose in the philosophical literature; it has been claimed that the location of transient dispositions is not fundamentally intrinsic (Smith 1977). If an object can acquire or lose a dispositional property then the "change in the world" that elicits this need not (but can) be intrinsic to the entity in question. The change may occur in the implicit environmental background, implicating a wider net of causal conditions that serve as the basis for the disposition. A lineage without the property of exploratory behavior, advantageous in fluctuating environments, may become evolvable$_R$ if the environment becomes highly stable. Therefore, external factors should be included in the causal base of the disposition. It appears impossible to ascribe a disposition to an entity without (at least) an assumed environment; certain dispositional properties are not identifiable with the intrinsic structure of the entity manifesting the disposition.

This line of thought directs us to ask whether or not extrinsic or environmental properties need to be included in the causal base of evolvability$_R$. Consider geographic range in marine invertebrates, which shows population level heritability and is arguably a cause of differential species duration (Jablonski 1987). Mollusk species with greater geographic ranges are better able to survive through large extinction events. In what sense is geographic range an intrinsic property of a population? It is not intuitively inside the individual organisms within a population and it is usually

2. Thus, there is no unique "causally operative sufficient condition" for the manifestation of evolvability (cf. Prior, Pargetter, and Jackson 1982).

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understood to be "a complex interaction of numerous intrinsic and extrinsic factors" (1987, 362), such as migratory abilities and landscape topography. What if evolvability$_R$ for a group of bivalve mollusks was due to a combination of modularity and geographic range? The environment does not allow or prevent the occurrence of the manifestation; it jointly determines the nature of the disposition. Two duplicate populations with near identical intrinsic conditions are not necessarily equally disposed to evolve (cf. Lewis 1997, 148).[3]

Whether evolvability$_R$ always involves extrinsic properties is an empirical question. Minimally, the burden of proof shifts to the advocate for wholly intrinsic dispositions who must articulate a story about evolvability$_R$ while assuming "normal" background conditions across geological time, a *ceteris paribus* clause that appears less than benign. Evolutionary change has taken place against an ever-changing background of climate and competition. Correlations between extinction and diversification events in evolutionary history and large-scale environmental changes remind us that a significant property underlying a lineage's capacity to evolve may be external to the population itself (Hoffman and Parsons 1997). Empirical studies of evolvability are also indicative of this point. Mutation rates in an RNA virus reveal a constraint on evolvability from the adaptive landscape; the ability to evolve is not just a function of generating genetic variation (Burch and Chao 2000). Fluctuating asymmetry is highly dependent on environmental stress conditions, which may significantly affect its evolutionary potential (Van Dongen and Lens 2000).

Another reason to question intrinsicality is the contribution of extrinsic factors to the origination (or loss) of the capacity. If over millions of years the origin of evolvability$_R$ were to require particular environmental conditions, then an argument could be made that these extrinsic factors are causally determinative of the capacity. Notice that this is not simply a claim that extrinsic factors lead to an alteration of intrinsic properties that then confer evolvability$_R$. Compare the case of an iron rod that becomes fragile via oxidation processes; the external atmospheric conditions induce a change in the intrinsic (chemical) properties of the rod, which thereby acquires the disposition. In the case of evolvability$_R$ *no change in intrinsic properties is necessary* to acquire the disposition, and external factors are rightly understood as comprising the causal base rather than as triggering conditions for the disposition. The feedback structure of the causal relations are critical for evolvability$_R$, which can be gained and lost, while the iron rod could not lose the disposition of fragility through long-term exposure to reducing conditions.

3. This is even more poignant when considering extrinsic biotic factors such as species interactions that engender coevolutionary dynamics (see, e.g., Thompson 1994).

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That evolvability$_R$ can have a causal base composed of intrinsic and extrinsic factors directs us (briefly) to the issue of the *causal efficacy* of dispositions. Some philosophers argue that dispositions are causally impotent; causal efficacy is located in properties of the causal base, such as modularity (Prior, Pargetter, and Jackson 1982). Is evolvability a genuine cause in evolutionary history or merely the outcome of evolutionary processes? Selection operates on short-term benefits to organisms in populations while evolvability$_R$ is usually of long-term benefit to a lineage. Has there been clade-level selection for evolvability$_R$? Although some have argued to this effect (Gerhart and Kirschner 1997), assessing the cogency of the argument is difficult; though possible in principle, its infrequency potentially signals relative insignificance for evolutionary history (Wagner, Chiu, and Hansen 1999). Because many discussions of evolvability focus on intrinsic properties of organisms, the significance of the environment can be construed as mere triggering conditions; the intrinsic disposition to evolve is manifested under particular environmental regimes. Alternatively, if external selection factors are the primary engine of evolutionary change, intrinsic properties of organisms are minor premises in the argument for why we observe a pattern of biological diversity over time. If we reject the intrinsicality of evolvability a third possibility emerges. The causal efficacy of evolvability is jointly determined by intrinsic and extrinsic factors, requiring an understanding of evolvability$_R$ in terms of both types of properties.

If the foregoing analysis is correct, it leaves us with the following dilemma. If dispositions necessarily have intrinsic causal bases, then those cases of differential lineage success that involve extrinsic properties are not technically evolvability$_R$. Any appeal to extrinsic conditions are not claims about the properties of the lineages, maybe because we define intrinsicality to exclude fitness differences between groups due to extrinsic factors, and thus the differential success of some clades is the result of environmental factors, not evolvability$_R$. This may force us to retract ascriptions of evolvability if these kinds of extrinsic factors are fairly ubiquitous, signaling the need for more empirical studies. On the contrary, we can admit that the causal base of evolvability$_R$ can contain intrinsic and extrinsic components and is still a probabilistic disposition to evolve. We could introduce a distinction between intrinsic and extrinsic components of evolvability$_R$, clarifying empirical research on the disposition. Although I believe this second option is more natural, it is radical in that it undercuts the common philosophical assumption of the intrinsicality of dispositions.[4] The plausi-

4. This point is also relevant to philosophical accounts of capacities developed explicitly from attention to scientific practice. If we seek a "peculiar kind of [experimental] repeatability that . . . requires a kind of permanence of behavior across varying external conditions that is comparable to that of an essence" (Cartwright 1992, 51), then the possibility of extrinsic factors in the causal base is intentionally ignored.

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bility of this assumption may derive from extended attention to a small set of examples that have intuitively intrinsic dispositions and are not thought of as population phenomena. Importantly, challenging the assumption of intrinsicality via evolvability$_R$ invites us to revisit traditional analyses of solubility and fragility.

4. Conclusion. The status of evolvability is intriguing precisely because it is located in the nexus of ongoing biological investigation. I have isolated three distinct but compatible approaches to evolvability (computational, theoretical, and empirical) and distinguished between evolvability$_U$ and evolvability$_R$, noting that evolvability$_R$ is primarily in view. Evolvability$_R$ is a transient disposition in that it can be gained or lost when particular properties of its causal base change. Recognizing that evolvability is a capacity of populations rather than individuals leads us to reconsider the philosophical assumption of the intrinsic location of dispositions. I have argued that the probabilistic disposition of evolvability instantiated by populations or groups is not wholly definable in terms of intrinsic properties, thus calling into question demands that dispositions be intrinsic to objects. The differences between causal processes at the population and individual level contribute to this conclusion.

Re-examining the intrinsicality of evolvability raises issues about the presumed ontology of philosophers and scientists. The ascription of an "intrinsic property" to an "entity" is within the tradition of substance-attribute ontologies. Maybe an adjustment of our presumed ontology is needed to understand dispositions in contemporary biology. It has recently been argued that a dualistic ontology of entities *and* activities is required to capture the nature of theorizing and explanation in molecular biology and neuroscience (Machamer, Darden, and Craver 2000). Attention to this metaphysical claim might elucidate evolvability as an intrinsic or extrinsic "property" of entities (modules, temperature, and conspecifics) and their respective activities (morphogenesis, thermoregulation, and competition). The recommendation to critically re-evaluate the assumption of intrinsicality in the philosophical literature may have far-reaching implications.

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