DISCUSSION: FROM INDIVIDUALS TO ECOSYSTEMS; THE PAPERS OF SKELLAM, LINDEMAN AND HUTCHINSON

1. Introduction. To many scientists, the inherently quantitative nature of ecology is self-evident. However, the debate between the mostly empirical field biologists *vs* theoreticians on the usefulness of mathematical models in ecology has a long history (MacIntosh, 1985)—and it is hardly resolved today. The papers of Lindeman (1942), Hutchinson (1957), and Skellam (1951) were conceived during one of several periods in this century of renewed interest in quantifying ecological process.*

Each paper deliberately imposed formal, mathematical structure on disciplines that the authors considered to be mired in controversies because they lacked quantification. In fact, Evelyn Hutchinson's entire career has been devoted to imposing formal theory on ecological musings; his own interests have been wide-ranging but always quantitative. Hutchinson mentored many famous students, who collectively represented his many facets and who made permanent impressions on the field of quantitative ecology. Although Lindeman was not his student, Hutchinson none the less shepherded Lindeman's landmark (and final) 1942 paper through negative reviews and saw that the paper was published posthumously. Hutchinson was also attracted to Skellam's quantitative approach and incorporated Skellam's results in the 1957 paper discussed here.

We review the three papers in separate sections. The three papers are tightly linked, despite treating disparate subjects. Each of the three demonstrates the success of a more reductionist approach to ecological problems. Lindeman's (1942) and Hutchinson's (1957) papers both represent watersheds in ecological research (ecosystem and community ecology, respectively) that produced volumes of brilliant work. Yet, each of these new directions in ecology ultimately stalled, we would argue, because they tried to explain higher-level patterns in ecosystems and communities without examining in sufficient detail what individuals and populations were doing. In contrast, Skellam (1951)

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* Hutchinson (1957, p. 416) wrote: "It is not necessary in any empirical sense to keep an elaborate logicomathematical system always apparent, any more than it is is necessary to keep a vacuum cleaner conspicuously in the middle of a room at all times. When a lot of irrelevant litter has accumulated the machine must be brought out, used and then put away" and Skellam (1951, p. 196) wrote: "Nevertheless, biologists as a whole have been reluctant to develop the analytical as distinct from the purely statistical . . .".

focused primarily on individuals in populations, and his work presages some of the most active areas of population biology today.

2. Birth of Ecosystem Ecology and its Relation to Community Ecology. Lindeman's (1942) paper is acknowledged as the beginning of formal ecosystem theory (MacIntosh, 1985). Here we present our interpretations about the bifurcation of ecosystem and community ecology, which can be dated directly to Lindeman's and Hutchinson's papers.

The early practitioners of ecology were interested in all of the various subdisciplines later represented by autonomous specialties. Theoreticians who predated Lindeman and Hutchinson, primarily A. J. Lotka and V. Volterra, and experimentalists such as G. F. Gause, were interested both in population dynamics and in energy flow through ecosystems (Lotka, 1925; Gause, 1934). The work of Lotka, Volterra and Gause provided the foundation for modern-day population and population-based community ecology (e.g. Cody and Diamond, 1975; Diamond and Case, 1986); indeed the population models of Lotka and Volterra are as alive today as they were in the 1920s and 1930s. Lindeman's ideas arose in an intellectual environment permeated with discussions by plant ecologists on what determines the distribution and abundance of plant species (e.g. Tansley, 1935; Clements and Shelford, 1939; Clements, 1916); today's population-based community ecology and ecosystem ecology each have strong Clementsian overtones (e.g. Strong et al., 1984; Price et al., 1984; MacIntosh, 1985). The beginning of ecosystem ecology were also heavily influenced by limnology and aquatic ecology; Lindeman's (1942) paper featured his doctoral work on Cedar Bog Lake, solidly in the tradition of early ecosystem ecology (e.g. Odum, 1953). Hutchinson was a limnologist, and he nearly single-handedly brought forth the brand of population and community ecology practised today. At the same time, he was deeply optimistic about Lindeman's conceptual breakthroughs in quantifying the energy pathways in lake ecosystems.

From this common intellectual ground arose two nearly separate and uncommunicating branches of ecology: ecosystem ecology and population and population-based community ecology.* Only a few ecologists bridged the gap (e.g. C. S. Holling, R. L. Kitching, S. A. Levin, L. B. Slobodkin, F. E. Smith). Otherwise, the voluminous literatures of the two fields are nearly separate, and students trained in one emerge from their studies largely ignorant of advances in the other. Yet the two fields share one name, and each declared itself as a "revolution" in ecology! Ironically, the same early ecologists set the two fields in motion.

What happened? What does the future hold? Most interestingly, Lindeman's ecosystem ecology had a bright future that most agree failed to

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* We will drop this awkward expression, but the distinction between early community ecology, practised by plant ecologists and limnologists, which was much more population-free, and present community ecology, which is derived from population ecology, needs to be kept in mind.

materialize (e.g. Foin and Jain, 1977; MacIntosh, 1985; Watt, 1975). Discussions on the fading of ecosystem ecology's bright star (specifically studies of the flow of energy and nutrients and descriptive mega-models of ecosystems) range from the efficacy of reductionism (population/community ecology) *vs* holism (ecosystem ecology), hypothetico-deductive *vs* inductive approaches, and mathematical methodology (MacIntosh, 1985; Watt, 1975).

Here, we develop some thoughts on the role of reductionism in ecology in understanding the unrealized hopes of Lindeman and in charting a future course for the study of communities and ecosystems.

Hutchinson was most excited about the prospect of Lindeman's work of understanding the structure of entire ecosystems by reducing them to "pairs of numbers" describing energy flow (Addendum to Lindeman, 1942). Hutchinson posed questions (not yet solved) that arose in Lindeman's work such as "What determines the length of food chains?" Yet Hutchinson himself represents the bifurcation of how this question, and ones similar to it, were approached by ecologists. From this point, Hutchinson's own work never lost sight of the importance of populations as components of ecosystems. His interest in energy flow per se (although still firmly attached to population interactions in food webs) seems to have petered out with a widely unread paper by his student Robert MacArthur (MacArthur, 1955).

Ecosystem ecology meanwhile pushed populations, and their component individuals, further and further into the conceptual background of its studies. Studies of the structure of entire food webs have a tradition of lumping whole kingdoms, subkingdoms and classes (e.g. bacteria, algae, zooplankton, copepods) into a single position in the web (Cohen *et al.*, 1990). However, this lumping of component populations into a single ecosystem "entity" was not only complete and deliberate, but seemed desirable by mainstream ecosystem ecology.

Clearly, at some level the structure of food webs is constrained by physical laws governing energy transfer and chemistry of inorganic nutrients, and understanding these constraints will be necessary to explain the broadest of ecological patterns. However, as long as ecosystem ecology is biology (and many components are not), it still falls under the Darwinian paradigm. Because ecosystem ecology largely eschewed populations, natural selection was not readily available as an explanation for patterns in ecosystems. Evolution enters into explanations of ecosystem patterns (when it does) with selection above the species level: ecosystem, community and food-web selection. For example, Odum and Biever (1984) postulated that plants like to be eaten by herbivores (in an evolutionary sense), because of indirect effects through the entire web that "enhance the welfare of primary producers and contribute to the homeostasis at the ecosystem level" (Odum and Biever, 1984). Lessons from the study of group selection are appropriate here (Williams, 1966; Wade, 1977; Slatkin and Wade, 1978; Wilson, 1980). To learn if ecosystem selection occurs

and if so, if it is strong enough to be felt above individual selection, we will need more precise mechanisms (including a formal theory) to replace naive or superficial postulates (e.g. Odum and Biever, 1984; O'Neill *et al.*, 1986).

Nonetheless, a number of scientifically productive areas of ecology remain "gene-free", so one might want to look further to explain why ecosystem ecology fails to provide convincing mechanisms for the patterns it describes. We believe that part of the problem is a focus on "flows" to the complete exclusion of component individuals and populations in ecosystems. Schoener (1986a) presents a lengthy discussion of whether explanations of patterns in higher levels of biological organization such as populations and communities can be reduced (e.g. scientific reductionism *sensu* Nagel, 1961; Wimsatt, 1980) to those in lower levels of organization, primarily the individual. Schoener concluded that some community-ecological patterns were reducible to factors affecting individuals through the pathway of communities→populations→individuals and others directly from communities→individuals.

We suggest that ecosystem ecology, as originally conceived by Lindeman and his predecessors, remains alive and well where studies attempt to reduce patterns along either of these pathways. Two examples of fields in which the questions originally posed by Lindeman are pursued with a much greater explanatory power than provided by rules of energy and nutrient flow are the following:

(1) The study of food webs is one that lends itself to bridging population–community ecology and ecosystem ecology, and that is exactly what is happening. Population ecologists are studying the population dynamics within food webs and asking many of the same questions as ecosystem ecologists (May, 1975; Pimm, 1982; Schoener, 1989b). For example, Pimm's (1982) book summarizes study of model food webs composed of populations of Lotka–Volterra plants, herbivores, omnivores and detritivores and Nicholson–Bailey parasites. Better predictions of real food webs might be obtained with more mechanistic formulations that incorporate the behavior and physiology of individuals. However, even Pimm's preliminary results provide more satisfactory answers to question such as "What determines the length of food chains? Are complex food webs more stable than simple ones? Why are there so few species that eat both plants and animals (don't forget the insects when pondering if this statement is true; but see Schoener, 1989b)? What determines predator/prey ratios?" Mechanisms center on population stability and how it constrains the design of food webs (Pimm, 1982; Schoener, 1989b).

(2) Patterns in communities of organisms that are relatively more influenced by the physical environment than the biotic one may be more likely to be directly reduced to factors affecting individuals. A prime example is woody plant communities, because their component individuals are so long-lived, with lifespans bordering on geological time [e.g. *Pinus longaeva*, the bristle-

cone pine (La Marche, 1969) or cloning species such as the creosote bush, *Larrea* (Vasek, 1980)]. With mean generation times in these woody plants in the hundreds or thousands of years, hundreds or thousands of generations of herbivores will have lived and fed upon them (e.g. Betancourt *et al.*, 1990). Meanwhile, glaciers come and go, volcanoes erupt, and water and wind rearrange the landscape—causing the physical environment to fluctuate widely (Elliot-Fisk, 1987; Thompson and Mead, 1982). Population-level processes in such species are very slow compared to the rest of the ecosystem they support and even (relatively speaking) to the landscape that supports them (Davis, 1986; Ellior-Fisk, 1988; Jennings and Elliot-Fisk, 1991). The dynamics of the population, and its interaction with others, surely must be secondary to the influence of the physical environment directly affecting individuals.

3. The Golden Years of Community Ecology: the Rise and Fall of Limiting-similarity Theory.   Hutchinson's (1957) paper, despite its inauspicious title ("Concluding Remarks") launched an academic generation of inquiry on what determines the structure and function of communities. The intelligent uninitiate might well question whether the difference between community ecology and ecosystem ecology hinges somehow on the semantics of naming the unit of study in the two fields. However, the Hutchinsonian community differed from the Lindemanian ecosystem in many ways (Hutchinson, 1957; 1959). It was smaller and taxonomically more narrowly delimited. The Hutchinsonian community was, implicitly, fairly high on the food chain—up near or at the very top. Species in a Hutchinsonian community were less influenced by the physical environment that by the other species in this narrowly defined unit. Thus, the Hutchinsonian community was a single, horizontal slice up at the top of a food web—only a small fraction of an ecosystem and not a very representative one at that. In such a context, interspecific competition emerges as the most interesting determinant of community structure.

This was no coincidence; Hutchinson's "Concluding Remarks" were his attempt to shore up a long period of empirical ecology purporting to demonstrate the "Gause–Volterra Principle". The competitive exclusion principle, due to Gause's experiments and Volterra's and Lotka's simple models of them, stated that two species cannot occupy exactly the same niche and coexist (Hardin, 1960). For more than a decade before Hutchinson's paper, field ecologists had been charting all the differences that allowed sympatric congeners to coexist. The tautology of this exercise escaped no one, and Hutchinson's "Concluding Remarks" featured a mathematical formalization of the concept "niche" that would allow the tautology to be broken.

Perhaps the most important feature of Hutchinson's formalization is the precise quantification of the niche (see also Schoener, 1989a). Hutchinson conceptualized a multidimensional niche, each dimension of which was a

continuous variable of some resource or other quantity of importance to individuals in that population. A niche dimension could be physiological (temperature or salinity tolerance), spatial (distance from a stream, height in the forest canopy) or dietary (size of a given food type). Such a niche earned the prodigious name of "n-dimensional hypervolume". While not all factors important to organisms could be so conveniently quantified, this concept allowed Gause's principle to be rephrased as a testable hypothesis. The question became: "Just how similar can two species be and still coexist?" or, "Is there a limit to how similar two species can be and still coexist?" (MacArthur and Levin, 1967).

The quest for the so-called "limiting similarity" began with the formal, if not overly simple, models of Lotka and Volterra. In addition to the convenience of their well-studied mathematical properties, use of these equations was fitting because they inspired Gause (and vice versa) in the first place. MacArthur and his colleagues (MacArthur and Levins, 1967; MacArthur, 1972; May and MacArthur, 1972; May, 1975; Roughgarden, 1974) provided the theoretical basis for predicting some hypothetical niche difference which would just permit coexistence, hence the "limit to similarity". MacArthur in particular turned out a set of pseudo-precise numbers, such as a limiting overlap (Gause's competition coefficient turned graphical by Hutchinson's hypervolume concept) of 0.544 or a limiting ratio of niche distance to niche width (d/w) of 1.1, $\sqrt{2}$ or 1.56 (depending on how you reasoned it). Such predictions were received with much skepticism because they were so model-dependent and patterns in Nature exhibit so much noise. What was the range of values that allowed you to confidently reject the hypothesis?

Other approaches were taken to get out of this fix. Roughgarden (1974) attempted to produce a range of predictions, depending on the type of competitor, foreshadowing what we see as the only productive route to investigate community-wide patterns of competition (more below). May's work with MacArthur (May and MacArthur, 1972; May, 1975) searched for a robust limit to similarity, one that would be more easily tested with field data, but much of this work was equally model-dependent (Turelli, 1978, 1981; see also Abrams, 1983).

Alternatively, another paper of Hutchinson's (Hutchinson, 1959: "Homage to Santa Rosalia") provided an approach that many hoped was more testable with data at hand, albeit less direct. Hutchinson proposed his famous morphological ratios (1.2–1.4 in a relevant linear dimension), assuming that morphology related directly to resource utilization and therefore niche dimensions. The idea behind the Hutchinsonian ratios was the same as that behind limiting similarity: interspecific competition would adjust niche positions and widths* until niches were regularly (non-randomly) arrayed along niche dimensions (Schoener, 1974).

* Either in ecological time by invasion and Gausian competitive exclusion or in evolutionary time by ecological character displacement (Roughgarden, 1976; Slatkin, 1980).

Hutchinson's two seminal papers (1957, 1959) led to two decades of data collection on resource utilization and morphological ratios and to innumerable Ph.D. theses (including one of ours—C.T.). Yet this mountain of data revealed little about whether a limit to similarity existed, much less what it was for any given system—very much like the period preceding Hutchinson (1957).

The mountain of data did reveal rich detail, that was not completely idiosyncratic, about many associations of species. This golden age of community ecology has also been analyzed in some detail (Colwell, 1984; Salt, 1983; MacIntosh, 1985), which we do not wish to review here. Rather, we wish to make a single point: Community ecology after its bifurcation from ecosystem ecology suffered from the same flaw in which communities were as "black boxes" just as ecosystems had been viewed. Although community ecologists tried to reduce communities to populations, the stopped short of reducing populations to component individuals, thereby still viewing component populations as black boxes (also see Schoener, 1986a).

By failing to reduce communities to individuals, community ecology during the golden age failed to recognize that the many different mechanisms of interspecific competition could produce vastly different community-wide patterns. In fact, only one type of competition (exploitive or scramble) was ever investigated by limiting similarity models based on the Lotka–Volterra equations. Hutchinson stated this in his "Concluding Remarks" in a list of "Cases where the Volterra–Gause principle is unlikely to apply", and the more mechanistic competition models of Schoener (1976) bear him out.* Subsequent field experiments on interspecific competition revealed a multitude of different mechanisms of competition (Schoener, 1983), each of which might produce its own characteristic community-wide pattern.

Community ecology has entered a new age (cf. Colwell, 1984) of "particularization", a period dominated by studies of the individuals that make up the populations that make up communities (e.g. Schoener, 1986b). It is an exciting time for community ecology, when biological detail can be fully appreciated and not brushed away as statistical noise. How much of this will be "irrelevant litter" (Hutchinson, 1957) remains to be seen, when the next wave of quantification and theory is ushered in.

4. Individual Movement and Population Growth. Unlike Lindeman or Hutchinson, Skellam (1951) began with a focus on the individual and considered the effect of individual behavior on population dynamics. Skellam's paper is both a masterpiece of applied mathematics and a unique contribution to biology because of the variety and depth of topics that it covered:

* Skellam's (1951) paper contained the other conditions where the Volterra–Gause principle was unlikely to apply.

(i) *Random dispersal* in which Skellam showed the connection between random walks and diffusion processes.

(ii) *Dispersal of small animals* in which the random dispersal model is tested using data on the spread of the muskrat in central Europe.

(iii) *Dispersal with population growth* in which dispersal models are incorporated into models of population growth (also see Kiersted and Slobodkin, 1953). If $p(x, t)$ is the population density at point x at time t, then under the assumption of *linear growth*

$$\frac{\partial p}{\partial t} = \frac{1}{2} a^2 \frac{\partial^2 p}{\partial x^2} + rp. \tag{1}$$

Here a^2 is a measure of the rate of dispersal and r the per capita rate of population growth. Skellam solved equation (1) for three cases, determined by the conditions at the boundary of the habitat. With *logistic growth*, equation (1) is replaced by

$$\frac{\partial p}{\partial t} = \frac{1}{2} a^2 \frac{d^2 p}{\partial x^2} + rp\left(1 - \frac{p}{K}\right). \tag{2}$$

This is, of course, also known as Fisher's equation and is connected to Turing's work on developmental models (Murray, 1990). We thus see that the mathematical method linked population genetics, population ecology and development biology with a common conceptual picture. Skellam also introduced a model for population decay called the *negative logistic* in which equation (2) is replaced by

$$\frac{\partial p}{\partial t} = \frac{1}{2} a^2 \frac{\partial^2 p}{\partial x^2} - g^2 p\left(1 - \frac{p}{K}\right). \tag{3}$$

The steady-state solutions for equations (2) and (3) were presented in a number of cases, again determined by boundary conditions and parameter scalings. Here Skellam concluded that "Solutions in terms of elliptic functions are obtained in a similar manner after making appropriate substitutions" (p. 205) and pointed out that population decay with immigration could also be considered by a modest modification of his results.

(iv) *Linear growth in two-dimensional habitats* in which equation (1) is extended to two spatial dimensions. By assuming circular symmetry, Skellam constructed eigenfunction expansions under five different assumptions about the nature of the boundaries. These solutions involve Bessel functions, classical special functions of applied mathematics.

(v) *Logistic growth in two-dimensional habitats*, the extension of equation (2) leads to the study of non-linear, second-order differential equations. Skellam

outlined an iterative method for the solution of this equation and described a number of its properties, including stability of steady states.

(vi) *A model of seed dispersal* in which the previous dispersal models were generalized to consider annual plants, as an example of an organism that grows in discrete time. Here, the analog of the Gaussian model of dispersal is the Poisson model. We assume that the world is divided into cells and let X_n denote the fraction of cells that are occupied by plants in generation n. Then the probability that a cell does not obtain a viable seed from parents in generation n when the fraction of occupied cells is $1 - \exp(-RHX_n)$, where R is the reproductive capacity of parent plants and H is a measure of habitat suitability. This leads to the difference equation

$$X_{n+1} = 1 - \exp(-RHX_n). \tag{4}$$

This equation is, of course, connected to Nicholson–Bailey host–parasitoid dynamics and to the dynamics of disease (see Anderson, this volume). Skellam showed that when RHX_n is small, equation (4) may be approximately solved by a conversion to a Ricatti-like difference equation and then generalized the result to consider competition between two species of plants in one or two habitats.

This paper forces people to think about populations growing over both *space* and time and to think in terms of stochastic, rather than deterministic, phenomena. It links, in one way, what individuals do (random motion) with what populations do (growth) within a single conceptual framework. It is part of the "probabilistic and materialistic" revolution begun by Darwin (Simberloff, 1980), continued by Thomas Park, but not yet complete (e.g. the latest contribution is given by Costantino and Desharnais, 1991). In this revolution, states (of organisms, for example) are as important as flows (of energy, for example) and indeterminacy is the rule rather than the exception. Ideas concerning movement over space and time and stochasticity have infected part, but not all of every area of population biology, including experiment and theory. Reviews of contributions through the late 1970s are found in Okubo (1980), who deals mainly with mathematical questions, and Swingland and Greenwood (1983) who deal mainly with biological aspects of animal movement.

We now briefly describe some more recent work, which is rooted in the intellectual heritage that Skellam provided.* Our intention is to be illustrative rather than comprehensive.

Clines, gene flow, and speciation.   The spatial distribution of alleles may often be governed by equations similar to equations (1)–(3) and this can lead to

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* It is especially ironic that, even though Skellam provided such a rich intellectual heritage, he is not even mentioned in most ecology textbooks or in MacIntosh's history of ecology.

hybrid zones, which are spatially narrow regions of hybridization separating populations that are more or less genetically distinct. We begin with the question on establishment of an advantageous mutant in a spatially distributed population (Barton, 1987). Population dispersal models can then be used to study the maintenance of hybrid zones and barriers to gene flow, and mechanisms of speciation (Barton and Hewitt, 1989). Rouhani and Barton (1987) have shown how path integrals, a function space (Schulman, 1981) interpretation of equations (1)–(3), can be used to study the rate of transition between adaptive peaks for populations distributed over one- or two-dimensional spatial regions. Finally, Pease et al. (1989) have linked random dispersal models directly with quantitative genetics (Bulmer, 1985) by coupling a dispersal equation with a model for phenotypic evolution. This is done by replacing r in equation (1) by the log of the per capita per generation growth rate at a particular spatial point and time and then incorporating a similar diffusion equation for the change of the mean phenotype over space and time.

Dispersal in patchy environments.   Skellam's fundamental contribution was to describe the simplest, yet relevant model of population dispersal. Recent work has extended this simple model in a number of directions. For example, the model (1) assumes that increments in position are independent of previous experience. Kareiva and Shigesada (1983) extended this idea by predicting movement patterns in correlated random walks and then tested their ideas on motion of cabbage butterflies *Pieris rapae*, using data described by Root and Kareiva (1984). Levin et al. (1984) extended Skellam's model of seed dispersal by adding density dependence to dispersal and dormancy and computing the Evolutionarily Stable Strategies (Maynard Smith, 1982) of dispersal and dormancy. Other authors have considered the explicit nature of patchily distributed resources, including the size of patches and distances between patches and how that distribution affects dispersal and aggregation (e.g. Turchin, 1986, 1989).

Spread of invading organisms and biological control.   The success of biological control may depend, in large part at least, upon a sophisticated understanding of the spatial component of enemy–pest interactions (see Kareiva, 1989 for review). Skellam's ideas concerning random dispersal and population growth are beginning to find their way into the applied literature. For example, Sawyer and Haynes (1985) developed a model for the spatiotemporal dynamics of the cereal leaf beetle. Their model showed the importance of local features of fields in determining the spatial patterning of insects. A later study (Sawyer and Haynes, 1986) showed the importance of interfield regions as reservoirs for dispersing insects and how pest density was connected to the timing of crop growth. Bernstein et al. (1988) have begun to

incorporate explicit models of individual behavior (e.g. Mangel and Clark, 1988) into models for the dispersal and distribution of predators in a patchy environment. The advantage of models of this sort is summarized by Kareiva (1989, p. 224): "The main difference between my studies and those of other workers is that I strongly advocate the quantifying of rates of aggregation, not just the pattern of aggregation. In particular, I would advocate that more effort be made to connect explicitly the behavioural information to the population dynamics". Andow *et al.* (1991) summarize some of Skellam's work with respect to the spread of invading organisms and then apply the ideas to a number of particular cases including the muskrat, cereal leaf beetle, rice water weevil, and small cabbage white butterfly. Finally, Lubina and Levin (1988) have used an extension of equations (1)–(3), in which advection terms were added, to model the recovery and spread of the California sea otter.

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