# Holism and reductionism in biology and ecology

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## CHAPTER 10
## THE DISTINCTION BETWEEN HABITAT AND NICHE[67]

### 10.1 Introduction

In the next chapter I will discuss the reduction of the Lotka/Volterra competition model to modern niche theory. Before being able to do so, however, I will have to deal with the meaning of the term ’niche’. For the niche concept in modern niche theory is not the only niche concept being used in ecology and, more importantly, it is also not commonly recognized as the most adequate niche concept. There is not a single ecological handbook in which modern niche theory is recognized as such. Usually, various niche concepts are being used interchangeably. One of the purposes of the present chapter is to show that the niche concept in modern niche theory is the only adequate niche concept.

One cannot discuss the term ’niche’ without dealing with another term, which is at least as ambiguous, to wit ’habitat’. One of the problems besetting modern niche theory is the confusion of the concept ’niche’ with the concept ’habitat’. In spite of earlier attempts at elucidation (Hutchinson 1957; Odum 1971; Vandermeer 1972; Whittaker et al. 1973; Rejmanek and Jenik 1975; Grubb 1977, 1985; Alley 1982; Aarssen 1984; Giller 1984; Holt 1987; Schoener 1989), these concepts have remained controversial for decades and the distinction is still unclear. The situation is even so bad, particularly with respect to the niche concept, that the baby is thrown away with the bath-water (Chesson 1991; Shorrocks 1991).

Conceptual analysis of the ecological literature reveals that there are at least four different habitat concepts and as many niche concepts, where two of these habitat concepts correspond to two of these niche concepts. In addition, different habitat concepts correspond to different concepts of environment and to different concepts of biotope.

My purpose in this chapter is to sort out these various concepts and to suggest a clear assignment of terms. I will start with the habitat concept (10.2) and then discuss the niche concept (10.3). After that I will draw some conclusions pertaining to the difference between ’habitat differentiation’ and ’niche differentiation’ (10.4), two ’principles’ that are used to explain the coexistence or non-coexistence of species in communities (habitat differentiation leading to non-coexistence of species and niche differentiation being a mechanism of coexistence). These conclusions are remarkably close to what is commonly held about these principles, which I take to be strong support for the definitions of the concepts ’habitat’ and ’niche’ here proposed.

Because both ’habitat’ and ’niche’ are being defined in terms of environment (or of environmental, biotic and/or abiotic, variables), and because this is itself an extremely confusing term, I will have to start by discussing the several different meanings of the term ’environment’. In addition, because of the correspondences between different concepts of habitat and biotope, I will also discuss the various meanings of the term ’biotope’. For ease of exposition, I have used symbols to denote all these different concepts (E1, E2, ... for different concepts of environment; H1, H2, ... for different concepts of habitat, etcetera) and I have listed definitions of them in boxes. Readers who are unfamiliar with the subject, and who may get confused by all these concepts and symbols, may find relief in consulting these boxes. Boxes 2, 3 and 4 contain the various definitions of the terms ’environment’, ’habitat’

[67]This chapter is a slightly modified version of Looijen (1995).

and ’biotope’, respectively, which I have found in (or exerted from) the ecological literature. These definitions are discussed in sections 10.2.1 to 10.2.4, where I will argue in favour of the one definition and against others. The results of this, a list of recommended definitions, are presented in box 5. (Readers who do get confused by all the concepts I discuss are advised to consult box 5 first.) Similarly, box 6 contains the various definitions of the term ’niche’ which I have found in the ecological literature. These are discussed in sections 10.3.1 to 10.3.5, and the results, my recommended definitions, are presented in box 7.

## 10.2 Habitat

### 10.2.1 Different concepts of environment

Though undoubtedly the most common term in ecology, the term ’environment’ has seldom been defined explicitly. Where it is, the term is typically defined *relative to organisms*, as the sum total of abiotic and biotic factors surrounding and in some way affecting an organism or a group of organisms (for example Kendeigh 1961; McNaughton and Wolf 1973; Ricklefs 1973; Pianka 1974; Barbour et al. 1980; Andrewartha and Birch 1984; Krebs 1988; Freedman 1989; Brandon 1990, 1992). However, every ecologist uses the term also for a *place* concept, for the set of biotic and/or abiotic factors occurring at a certain place. In addition, when speaking of homogeneous or heterogeneous, fine-grained or coarse-grained environments, every ecologist uses the term environment also for an *area* characterized by distinct, more or less uniform, biotic and/or abiotic conditions. I will refer to these different concepts as E1, E2 and E3, respectively (box 2).

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|---|---|
| E1: | the sum total of abiotic and biotic factors surrounding and in some way affecting an organism or a group of organisms. |
| E2: | the set of biotic and/or abiotic factors occurring at a certain place. |
| E3: | an area characterized by distinct, more or less uniform, biotic and/or abiotic conditions. |

***Box 2***: Different concepts of environment in the ecological literature.

E1 defines the ’*Lebensraum*’ of an organism, the particular suite of biotic and/or abiotic conditions in which it lives (and to which, supposedly, it is adapted). This is identical to one particular concept of habitat (H1, see 10.2.2), namely the *standing place* or *living place* of an organism or a group of organisms. It is impossible, however, to explicate this concept (E1/H1) without appealing to E2 or E3, that is, without invoking the E2- or E3-environment that is supposed to make up the standing or living place of the organism or group of organisms. Therefore, to avoid circularity, if the concept of habitat is to be defined in terms of environment, ’environment’ should not be defined in the sense of E1.

E2 is based on the view that any arbitrary section of physical space (a place of whatever size) consists of, and can be characterized in terms of, a particular combination of values of abiotic and biotic variables, which is called the E2-environment of the place. Thus, what is termed an E2-environment is determined by what is considered a place. In the extremes, it may be the smallest perceivable section of physical space, but also the largest (that is, physical space in its entirety). In this sense, one speaks also of the earth’s environment. In what follows, however, I will presume that a place is a relatively small section of physical space (relative to the kind of organisms being studied), and I will use the term ’area’ for larger sections (an area being defined as a set of adjacent places).

E3 is based on the observation that there are, in any landscape, different areas with more or less clearly distinct suites of biotic and/or abiotic conditions. E3-environments are usually characterized in terms of broad categories of soil (such as terrestrial or aquatic, acidic or basic, sandy or loamy, rich or poor) or of vegetation cover (such as type of woodland or grassland, reed-marsh, mangrove, etcetera). In this sense, environments correspond to what some call habitats and others biotopes (H3, B3; see sections 10.2.2 and 10.2.4). Because abiotic and biotic conditions are often connected by most gradual transitions (’environmental’ gradients), it may be extremely difficult to delineate different E3-environments from one another (see chapter 9). Nevertheless, the areas occupied by E3-environments are more or less fixed by the uniformity (or similarity) condition. That is, generally, the variation of values of biotic and/or abiotic variables is smaller within than between E3-environments.

There is an asymmetry between E2- and E3-environments in that every E3-environment is an E2-environment, but not every E2-environment is an E3-environment. For any E3-environment occupying some area may be considered the E2-environment of that area, but the term E2-environment applies also, whereas the term E3-environment does not, to the sum of biotic and/or abiotic variables occurring at some place within that area.

In the rest of this chapter I will use the term ’environment’ (unless stated otherwise or when citing others) in the sense of E2, because it (and only it) allows the other concepts (E1, E3, to be called either habitats or biotopes; see 10.2.4) to be defined in terms of environment. More specifically, presuming a base set of places and a base set of abiotic and biotic variables, I will define an environment-type as a particular set (or combination) of values of abiotic and biotic variables, and I will assume that, at any one time, each place has an (one) environment of a certain type. Of course, at different times the same place may have different environments, and different places may have environments of either the same type or different types.

E3-environments (that is, habitats or biotopes), then, may be defined as sets of more or less similar (E2) environments, an E3-environment being (completely) homogeneous when it is comprised of a set of identical (E2) environments, and (more or less) heterogeneous when it is comprised of a set of (E2) environments which are (significantly) different from one another in the value of at least one abiotic or biotic variable (though not as different, generally, as they are from (E2) environments comprising other types of E3-environments).

### 10.2.2 Different concepts of habitat

Definitions of ’habitat’ in the ecological literature refer to at least four different concepts (box 3). The first of these (H1) is the concept of habitat as *standing place* or *living place* of an organism or a species, meaning the (E2- or E3-)environment or the set of (E2- or E3-) environments in which the organism or species lives (for example Kendeigh 1961; Hanson 1962; Odum 1971; McNaughton and Wolf 1973; Whittaker et al. 1973; Barbour et al. 1980; Krebs 1988, 1994).

The second habitat concept (H2) is that of the set of (E2- or E3-)environments meeting a species’ ecological requirements and tolerances, that is, the set of (E2- or E3-)environments in which the species could, but need not actually, live. This is the concept of habitat as *habitable place* or *suitable environment* for a species (for example Odum 1971; Whittaker et al. 1973; Whittaker 1975; Andrewartha and Birch 1984).

The third concept (H3) is the one of habitat as a particular kind of E3-environment within which *many species* may live. This concept corresponds to E3, but carries with it the connotation of being *suitable for many species* (for example Daubenmire 1968; Whittaker et al. 1973; Begon and Mortimer 1981).

The fourth concept (H4), finally, is the concept of habitat as the (E3?) *environment of a community* (for example Kendeigh 1961; Hanson 1962; Whittaker et al. 1973; Krebs 1988, 1994; Begon and Mortimer 1981). (Notice that many authors use the term 'habitat' interchangeably for two or more of these concepts.)

| | |
|---|---|
| H1: | the set of (E2 or E3) environments in which a species lives. |
| H2: | the set of (E2 or E3) environments meeting a species' ecological requirements and tolerances. |
| H3: | an E3-environment within which many species may live. |
| H4: | the (E3?) environment of a community |

***Box 3***: Different concepts of habitat in the ecological literature.

The question is, of course, in what sense 'environment' is being used in these definitions. Obviously, H3 refers to E3, but things are not that clear when it comes to H1, H2, and H4 On the one hand, the H1-habitat of an individual organism may well be the E2-environment of the place which is occupied by the organism, whence the H1-habitat of a species (population) would be the set of E2-environments of the places occupied by individuals of the species (population). This may or may not be an E3-environment. (A species' population may be restricted to a set of E2-environments within an E3-environment, but also range over two or more E3-environments.) On the other hand, this seems relevant only with respect to sessile species. With respect to motile species, even the H1-habitat of a single organism may consist of at least a set of E2-environments, and just as well be a set of E3-environments. Hence, the H1-habitats of species (populations) may just as well be sets of E3-environments as sets of E2-environments. Considering, however, that 'the set of E2-environments where individuals of the species occur' implicates 'the set of E3-environments where individuals of the species occur', but not the other way around (because the former is contained in, or a subset of, the latter), it seems safe to define H1 as the set of E2-environments in which individuals of a species live. Similarly, H2 may be defined as the set of E2-environments in which individuals of a species could (but need not actually) live.

The difference between H1 and H2 may be put by calling H2 the *potential habitat* of a species and H1 its actual or *realized habitat* (the latter being a subset of the former). An important implication of this difference is that habitat as H2 may be used (as one of many possible factors) to explain habitat as H1. That is, H1 is a descriptive concept, whereas H2 may be used as an explanatory concept. For given the ecological requirements and tolerances of a species, it is possible to determine whether or not some environment belongs to its H2-

habitat, hence to explain why it has the H1-habitat it has.[68] Naturally, if a species is absent from an environment even though this is considered to belong to its H2-habitat, its absence must be explained by other factors (for instance isolation).

H3 too may be used as an explanatory concept. H3 allows one to explain a species' presence in (or absence from) an area in terms of the habitat of the area being suitable (or unsuitable) for the species. This is the sense in which many biogeographers (for example Diamond 1975; see chapter 13) use habitat. The difference between H2 and H3 is, of course, that the former refers to the set of environments which are suitable to a (one) species, whereas the latter refers to a (one) E3-environment which may be suitable to more than one particular species.

What exactly is meant with H4 depends not only on the meaning of the term 'environment' but also on that of the term 'community'. It would go too far, however, to sort out all possible interpretations of H4 on the grounds of the various definitions of the term 'community'. Two remarks will have to suffice.

Firstly, it seems safe to say that the 'environment' of a community is 'the set of (E2) environments of the places occupied by all the individuals of the community'. This is in line with the definition of the term 'community' I have given myself in the former chapter, but it seems compatible with most other definitions as well. However, apart from its descriptive adequacy, there doesn't seem to be much use for this as a separate habitat concept. Secondly, on other definitions of the community concept, such as 'all the organisms living in a certain habitat or biotope' (where 'habitat' and 'biotope' are used in the sense of E3), H4 reduces to H3, in which case there is also no need for H4 as a separate concept. For this and other reasons, I will suppose in the rest of this chapter that H4 reduces to H3. (Notice that H4 reduces also to H3 when 'the set of environments of the places occupied by all the individuals of a community' constitutes an E3-environment.)

The major difference between H1 and H2 on the one hand and H3 and H4 on the other, is that the former are *species* concepts (relating to one particular species), whereas the latter are *community* (or many species) concepts. That is, habitats in the sense of H1 or H2 cannot be determined independently of a particular species, whereas habitats in the sense of H3 (and H4 in those cases where it reduces to H3) can. Also, whereas H3 and H4 allow many species to occupy a single habitat, H1 and H2 presuppose that *each species has its own unique habitat* and that there are as many habitats as there are species (not precluding, however, the possibility of habitat overlap).

### 10.2.3 Problems of ambiguity

To use the same term for such different concepts is, of course, confusing and may have more serious consequences. For instance, in a paper (*nota bene*) on the clarification of the terms 'habitat' and 'niche', Whittaker, Levin and Root (1973) end up suggesting the following 'definition' of habitat: "[the] *habitat* [of a species]" is described by "the species' population response to *habitat* variables within [the] *habitat* hypervolume [which the] species occupies [in the] *habitat* hyperspace defined by the [..] variables of physical and chemical environment

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[68]Of course, the explanatory power comes not from the application of the term 'habitat', but from knowledge of the ecological requirements and tolerances of species.

that form spatial gradients in a landscape or area" (Whittaker et al. 1973, p. 334; emphasis added).[69] This ’definition’ is unintelligible, of course, because the authors confuse at least two different habitat concepts: they aim to define the species concept (more specifically: H1), but their *definiens* refers to the community concept (H3).

A similar sort of confusion can be found in a well known ecological handbook (Begon et al. 1986), where it is stated on the one hand that "each organism’s habitat (..) is unique" (p. 513), presupposing H1 or H2, while a few lines later it is concluded that "a small woodland might be a heterogeneous habitat for a beetle attacking aggregates of aphids, a homogeneous habitat for a rodent collecting seeds from the woodland floor, and part of a heterogeneous habitat for a large, predatory buzzard ranging over a wider area of ground", where it is unclear whether H2 or H3 is being presupposed. Elsewhere, the authors note that "a woodland habitat, for example, may provide niches for warblers, oak trees, spiders and myriads of other species" (p. 74), clearly presupposing H3.

That things may get worse than confusion may be illustrated by the afore-mentioned (9.2.3) competitive exclusion principle (CEP). According to Begon, Harper and Townsend (1986, p. 260), the CEP may be read as: "If two *competing* species coexist in a stable *environment*, then they do so as a result of niche differentiation, i.e. differentiation of their realized niches. If, however, there is no such differentiation, or if it is precluded by the *habitat*, then one competing species will eliminate or exclude the other" (second and third emphasis added). Presuming that the terms ’environment’ and ’habitat’ co-refer, this boils down to roughly the same as: "Different species having identical ecological niches cannot coexist for long in the same habitat" (DeBach 1966, p. 184). However, if each organism (or species) has its own unique habitat, as the authors also hold, then ’coexistence in a habitat’ is a contradiction of terms, turning the CEP into a tautology (irrespective of whether or not the species have identical niches).

Things get all the worse when we find that the term ’niche’ is also being used for several different concepts, one of them being identical to the concept of habitat as the standing place or living place of a species (see section 10.3). Thus, with some exaggeration, the above formulation of the CEP may also be read as: ’different species having identical niches cannot coexist for long in the same niche’. Who knows?

### 10.2.4 Habitat and biotope

Clearly, these and similar problems can be resolved only by having unambiguous and mutually exclusive definitions of terms. Now the term ’biotope’ is being used interchangeably with habitat, the latter more in English and the former more in other European languages (box 4). In English, the term biotope is used for the ’environment’ of a community (that is, B1 = H4). In other European languages it is used for the set of environments which are suitable for a particular species (that is, B2 = H2). And in both English and other European languages, it is also used for "a topographic unit characterized by both uniform physical conditions and uniform plant and animal life" (Kendeigh 1961; see also Hanson 1962), that is, for particular kinds of E3-environments (that is, B3 = E3 = H3).

[69] I have changed the order of words in this quote, without, however, changing its ’meaning’.

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|---|---|
| H1: | the set of environments in which a species lives. |
| H2/B2: | the set of environments meeting a species’ ecological requirements and tolerances. |
| H3/B3: | an E3-environment within which many species may live. |
| H4/B1: | the (E3?) environment of a community. |

***Box 4***: Different concepts of habitat and of biotope in the ecological literature.

Thus, there are three biotope concepts, each of them corresponding to one particular concept of habitat. Leaving aside the concepts of habitat and biotope as the E3-environment of a community (H4 and B1) (assuming again that H4, and hence B1, reduces to H3), the above problems can be resolved, therefore, by assigning either the term habitat or the term biotope to the community concept (H3/B3/E3) and the other term to the species concept (H2/B2). The choice is more or less arbitrary (and, unfortunately, will always dissatisfy some people), but there are two reasons why, in my view, the term ’habitat’ is best used for the species concept.

In the first place, if we were to assign the term habitat to the community concept (H3/B3/E3) and the term biotope to the one species concept (H2/B2: potential habitat), the other species concept (H1: realized habitat) would be left out of account. Of course, one might invent a new term for H1 (for example: realized biotope), but it doesn’t seem wise to add yet another term to the already confusing vocabulary. It seems more appropriate, therefore, to assign biotope to the community concept (B3) and habitat to the species concept, where the distinction between potential habitat (H2) and realized habitat (H1) may be retained (or made explicit).

| | |
|---|---|
| environment: | the set, or combination, of (values of) biotic and/or abiotic variables occurring at a certain place (E2). |
| biotope: | an area (topographic unit) characterized by distinct, more or less uniform biotic and/or abiotic conditions (that is, a set of adjacent places having more or less similar environments) (B3 = E3 = H3). |
| potential habitat: | the set of environments meeting a species’ ecological requirements and tolerances (H2). |
| realized habitat: | the set of environments in which a species lives (H1). |

***Box 5***: Recommended definitions of the concepts of environment, biotope and habitat.

The second, more important, reason is that this or a like distinction between potential and realized *habitat* is required in order to formulate the concept of habitat differentiation. For habitat differentiation pertains to spatial differentiation of species such that each species ends up occupying only a subset of the set of environments which it could potentially occupy. In other words, the species’ realized habitats (H1) are subsets of their potential habitats (H2). Thus, habitat differentiation may be defined as reduction of habitat overlap such that realized habitat overlap is less than potential habitat overlap (but see section 10.4.1, for a slight qualification of this formulation). This concept would be much less easy to define if we were to use the term habitat for the community concept.

Box 5 summarizes the results so far. It provides a list of recommended definitions of the terms environment, biotope and (potential and realized) habitat which are separately unambiguous and jointly coherent and consistent.

## 10.3 Niche

### 10.3.1 Different niche concepts

There are at least four different niche concepts in ecology (box 6). The first of them (N1) originated with Grinnell (1917, 1924, 1928), who subsequently defined a niche as ’the place a species occupies in an association [that is, a biocoenosis, RL]’, ’the ultimate unit of habitat’, and ’the ultimate distributional unit within which a species is held by its structural and functional limitations’. To Grinnell, a niche was a ’place’ or ’space’ (recess) in a biocoenosis or ecosystem where a species could find food and escape from enemies (predators). Whether or not to his intention, this concept has been interpreted as equivalent to habitat as standing place, and has come to be known as the ’*habitat niche*’ or ’*place niche*’ (for example Odum 1971; Grubb 1977). There is no need to waste much time on this concept: if niche is equivalent to habitat, then ’habitat niche’ is a pleonasm and hence superfluous; and if niche is not equivalent to habitat, the question remains what the term ’niche’ refers to.

The second niche concept (N2) is the Eltonian *functional niche*: the *role* a species has in a community or biocoenosis, where with ’role’ is meant the species’ habits and mode of life and, specifically, its position in a food chain or web, that is, its relations to food and enemies (Elton 1927; see also Odum 1971; Whittaker et al. 1973). Elton developed the idea that biocoenoses are closely related groups of interacting species, where each species plays a certain role in the larger group, that is, fills a particular niche. Characteristic of his niche concept is, however, that the ’role’ played by a particular species may be played also by other species, or, in other words, that the niche filled by the one species may be filled also by other species. The ’role’ of the kestrel as a ’mouse-eater’, for example, may be played also by the buzzard. "For instance, there is the niche which is filled by birds of prey which eat small mammals... Or we might take as a niche all the carnivores which prey upon small mammals, and distinguish them from those which prey upon insects" (Elton 1927, p. 64). Odum (1971) tried to illustrate the difference between N1 and N2 by the terms ’address’ and ’profession’, respectively. Many have taken this to be the difference between habitat (address) and niche (profession).

The third niche concept (N3) is Hutchinson’s (1957) abstract *multidimensional* niche. Hutchinson distinguished between a species’ *fundamental* niche (later also called potential niche) and its *realized* niche. He defined the fundamental niche of a species as the hypervolume defined by the limiting values of all environmental variables, both physical and biotic, relative to the species, allowing it to survive and reproduce. This can best be pictured by starting with two environmental variables and supposing that for each variable there is a range of values to which a species is adapted and which allow it to survive and reproduce. When the two variables are plotted against each other, one obtains an area defined by the combinations of values of the two variables which allow the species to survive and reproduce. When a third variable is added, also with a range of values to which the species is adapted, one obtains a volume defined by the combinations of values of the three variables which

N1: the habitat niche or place niche, that is, the standing or living place of a species.
N2: the functional niche, that is, the intracommunity role of a species, its relations to food and other species.
N3: the multidimensional niche, that is, the hypervolume defined by the limiting values of all environmental variables relative to a species, allowing it to survive and reproduce (fundamental niche), or the subset of this resulting from interactions with other species (realized niche).
N4: the trophic niche or resource niche, that is, the full set of resources and resource states that meet minimal requirements for a species (potential niche), or the subset of this resulting from interactions with other species (realized niche).

***Box 6***: Different concepts of niche in the ecological literature.

allow the species to survive and reproduce. One can go on like this until all environmental variables relative to the species are included. The resulting hypervolume is, in Hutchinson's terminology, the fundamental niche of the species. Hutchinson defined the realized niche of a species as the subset of its fundamental niche resulting from interactions with other species, where he had in mind in particular competitors.

The fourth niche concept (N4) is in fact a restriction of Hutchinson's multidimensional niche to resource variables, where a similar distinction is made between potential and realized niche. The former may be defined as the full set of resources and resource states that meet minimal requirements for a species, the latter as the subset of this resulting from interactions with other species (but see section 10.3.5 for some nuances). This concept lies at the heart of mathematical competition and predation (resource-consumer) models (for example MacArthur and Levins 1964; Rescigno and Richardson 1965; MacArthur 1968; Levins 1968; May 1981; Pianka 1981; Glasser and Price 1982, 1988; Tilman 1982, 1988; Holt 1984, 1987; Abrams 1986, 1988a). It is also the concept of modern niche theory, which is, in fact, the family of these resource-consumer models. Unfortunately, however, though its popularity is increasing (see for example Pianka 1981; Bazzaz 1986; Schoener 1989), it has not yet been fully recognized as a separate niche concept.

### 10.3.2 Hutchinson's multidimensional niche

To many ecologists, perhaps the most, a niche is Hutchinson's (1957) multidimensional niche (N3). This may in fact be regarded as an amalgam of the 'habitat niche' (N1) and Elton's functional niche (N2). It has been described as "an evolved, multidimensional attribute of a species (..)" (Whittaker et al. 1973, p. 333), "the way a species is adapted, structurally, physiologically and behaviorally, to its environment" (Odum 1971, p.234). According to Hutchinson himself, it "will completely define [the species'] ecological properties" (Hutchinson 1957, p. 388). Hutchinson (1957) included in a species' (fundamental) niche "all ecological factors", "all environmental variables, both physical and biological, relative to [the] species" (p. 388), that is, both abiotic conditions, abiotic and/or biotic resources, and (though this may not have been his intention) other biotic factors (predators, parasites, competitors, etcetera). Thus, Hutchinson's niche concept is very comprehensive: it says just about everything about the ecology of a species. It is probably for that reason that the concept has become so popular. In my view, however, it is inadequate as a niche concept. In order to show this, I will have to extend a bit on modern niche theory and in particular competition theory.

In competition theory, which may be regarded as a special application of modern niche theory (see Glasser and Price 1982, 1988), it is assumed that (exploitation)[70] competition between species is the result of overlap of their potential (fundamental) niches, that is, of the fact that they make demands on the same set of resources. The theory states that when two species have identical niches, there are two possible outcomes of competition. The first possibility is that there will be niche differentiation, which means that the species switch over to different subsets of the set of resources such that realized niche overlap, and hence the intensity of competition, decreases. However, if this is impossible, for instance because the biotope is completely homogeneous or because there is only one resource, the only alternative is competitive exclusion of one of the species: the species with the lowest minimum requirement for the resource will be able to reduce it to a level which allows itself to survive but which is too low for the other species. In either case, the species' realized niches are subsets of their potential niches. (This applies also to the excluded species in the second case, since this species will not have a realized niche in the biotope).

Thus, the idea (which seems paradigmatic, but see Holt 1987) is that competition is the result of overlapping potential niches or, in other words, that potential niche overlap is a necessary (though insufficient) condition for competition, and that as a result of competition the species have realized niches that are subsets of their potential niches. For two reasons, Hutchinson's multidimensional niche concept (N3) is incompatible with this theory.

In the first place, it includes not only resources but also environmental conditions relative to a species (see Tilman 1982, and Abrams 1988b, for the distinction; see also Grubb 1985). This is incompatible with the view that niche overlap is a necessary condition for (exploitation) competition. For it allows different species to have overlapping niches without, however, being competitors, namely when niche overlap pertains only to non-resource variables, whereas (exploitation) competition occurs for resources.

In the second place, the multidimensional niche concept includes not only environmental variables that may be considered either resources or conditions relative to a species but also relations with other species, such as competitors. This is incompatible with the distinction between potential (or fundamental) niche and realized niche. For the latter is defined as the subset of the former resulting from interactions with other species. This is impossible if such interactions are already included in the species' (potential or fundamental) niche. Put differently, if relations with other species are already included in a species' (potential or fundamental) niche, then they cannot affect it such that a realized niche results (see also Aarssen 1984). Obviously, Hutchinson was unaware of this incompatibility in his definitions.

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[70]In ecology two types of competition are being distinguished, namely interference competition and exploitation competition. The former consists of direct interactions between species, such as threats, fighting and chasing in animals or, for instance, allelopathy in plants (the excretion of substances that are toxic to other species). The latter proceeds indirectly through exploitation of resources. The theory sketched in the main text pertains only to exploitation competition.

### 10.3.3 Elton's functional niche

Because the Eltonian 'role' niche (N2) is defined exclusively in terms of a species' relations with other species, it is inadequate for the same reason as is N3. This depends, however, on what is meant with a species' role in a community or biocoenosis. Elton meant by the term 'role' a species' position in a food chain or web, its relations to food and enemies. There would be no problem if this 'role' (niche) concept were restricted to food relations, or, more generally, to resource relations, but then in the sense of *resources being utilized by a species*, not in the sense of the species itself being a resource for other species or of the species competing for resources with other species. That is, the problem arises as soon as relations with other species *at the same or a higher trophic level*, that is, enemies and in particular competitors, are included. Clearly, if the enemy is a predator, then the species itself may be said to belong to the predator's niche, but not the other way around. This applies to any resource-consumer (prey-predator, host-parasite) system, where the relevant species is the resource and the enemy its consumer. And if the enemy is a competitor (in the exploitative sense), then, since competitors are, by definition, species that make demands on the same resources, the species and its competitor may be said to have overlapping niches, but it doesn't make sense to say that the one belongs to the niche of the other. If one allows for the latter, then any statement about competition as a consequence of overlapping potential niches, or about realized niches as a consequence of competition, becomes incoherent.

It should be noted, moreover, that a major application of niche theory is to explain (differences in) the structure of communities (and biocoenoses), such as species' number and composition, and relations between species. If niche theory is to have such applications, then the last thing one should do is to define a species' niche in terms of its relations to (all) other species in a community. For this would simply amount to defining niche in terms of community structure, making explanations of community structure in terms of niches essentially circular.

### 10.3.4 The resource niche and its difference from habitat

It follows from the above considerations that the term 'niche' must be restricted to resource utilization (N4) if niche theory is to be both internally consistent and compatible with competition theory. I think I am now also able to explain why, even apart from the 'habitat niche', 'the' niche concept has been and is being confused so often with 'the' habitat concept.

One should not conclude from the above criticisms that the multidimensional concept (N3) is useless, only that the term 'niche' should not be applied to it. The reason why the (this) niche concept has been confused so often with habitat is that, because of the inclusion of environmental tolerances, it indeed comes very close to the concept of habitat as defined above. For the multidimensional niche of a species may be regarded as a set of points in an abstract multidimensional ('niche') space, each point corresponding to a combination of values of biotic and/or abiotic variables - that is, an environment-type! - that would permit the species to survive and reproduce. In other words, it is the abstract set of all possible environment-types that meet the species' ecological requirements and tolerances. Thus, Hutchinson's multidimensional concept may be regarded as a more precise (set-theoretical), though abstract, formulation of the potential habitat of a species (H2: the set of environments meeting the species' ecological requirements and tolerances).

This can be nicely illustrated by Aarssen's (1984) definitions of (the Hutchinsonian) niche. Aarssen distinguishes between the potential and the available niche of a species, both of which are pre-interactive, and its realized or post-interactive niche. The potential niche is "a theoretical hyperspace of 'places' where a species could leave descendants defined by *all resource requirements and environmental tolerances* [of the species], but without reference to biotic interactions". The available niche is a "real 'place' (or set of places) in nature that is a subset of a species' potential niche (..). This is roughly *equivalent to habitat* and represents the real space where a species could theoretically leave descendants if there were no biotic interactions with other species". The realized (post-interactive) niche, finally, is a "real 'place' in nature where [the] species can leave descendents in spite of continued interaction with (..) other species" (all quotes from Aarssen 1984, p. 78; emphasis added).

Given the inclusion of environmental tolerances in his definition of potential niche, and assuming that with 'the set of real places' Aarssen means 'the set of environments occurring at certain places', the available niche of a species is the set of environments meeting the species' resource requirements and environmental tolerances, which is indeed equivalent to its (potential) habitat (H2). Analogously, his (Aarssen's, but also Hutchinson's) realized niche is equivalent to the realized habitat of a species (H1): the set of environments where the species actually lives (and can leave descendants).

However, if the concept of niche is restricted to resources, the available niche of a species (that is, its potential niche as defined by N4) is not equivalent to its potential habitat, but to the *restriction* of its potential habitat to the set of resources the species is able to utilize. Similarly, then, the species' realized niche can be defined as the restriction of its realized habitat to the set of resources the species actually utilizes.

### 10.3.5 Partial niches

Thus defined, however, it is necessary to make a distinction between the niche a species realizes in the absence of other (non-resource) species and the niche it realizes in the presence of other (non-resource) species. Vandermeer's (1972) notion of partial niches seem suitable for this, were it not that Vandermeer too did not restrict the meaning of the term niche to resource utilization. Given this restriction, however (Glasser and Price 1982, 1988), the term *0-th (zeroth) partial niche* can be used for a species' niche when its population size, and that of other (non-resource) species, is close to 0, that is, when there are no density effects, neither from the species itself nor from other (non-resource) species. The term *1-st partial* or *intraspecific niche* can then be used for a species' niche when its population size approximates the carrying capacity of the biotope[71] and when there are only intraspecific density effects. And the term *S-th partial* or *interspecific niche* can then be used for a species' niche in the presence of both intra- and interspecific interactions (where S may be 2, 3, 4, ... species).

The term realized niche has traditionally been used, by convention, only for the (interspecific) S-th partial niche of a species. In addition, it has been suggested that the 1-st

[71]Usually, one speaks of the carrying capacity of the environment or of the habitat but of course I must use the term biotope.

partial niche be referred to as the potential niche of a species, because it is the largest (or widest) niche a species can occupy in a given biotope (Glasser and Price 1982, 1988). This (that is, equating 1-st partial niche with potential niche, and S-th partial niche with realized niche) would have the obvious advantage of reducing the number of relevant niche terms. Unfortunately, however, it conflicts with the ordinary meaning of the terms ’potential’ and ’realized’ (indicating a possibility or (cap)ability as against an actuality). To apply the term ’realized’ only to the S-th partial niche would suggest that the 1-st partial niche cannot be a ’realized’ niche, whereas obviously, it is ’realized’ (in the ordinary sense of the word) if there are no interspecific density effects. To apply the term ’potential’ to this ’realized’ niche would be doubly confusing. Therefore, to avoid such confusion, I suggest that 0-th, 1-st and S-th partial niches all be viewed as realized niches, though as different forms, of course (the differences being indicated by the relevant prefixes), and as distinct from the potential niche (see box 7).

**Potential niche**: the full set of resources and resource states that meet minimal requirements for a species. This is equivalent to the restriction of its potential habitat to the set of resources the species is able to utilize.

**Realized niche**: the (restriction of its realized habitat to the) set of resources a species actually utilizes. The terms 0-th, 1-st and S-th partial niche refer to the niche a species realizes when it experiences, respectively, no intra- and interspecific, only intraspecific, and both intra- and interspecific density effects.

***Box 7***: Recommended definitions of the concepts ’potential niche’ and ’realized niche’.

### 10.3.6 Empty niches

One of the specific controversies resulting from the confusion of various niche concepts pertains to the question whether there are ’empty’ niches (see, for example, Whittaker et al. 1973; Kroes 1977; Pianka 1983; Giller 1984; Schmitt 1987). The answer to this question is also important with regard to the question whether there are ’incomplete’ biotopes or ’incomplete’ ecosystems, which in turn is of interest also with respect to nature conservation issues (Dekker 1990).

Whether it makes sense to talk of empty niches depends of course on the niche concept one uses. As mentioned, to Grinnell a niche was a ’place’, ’space’ or ’recess’ in a community or biocoenosis where a species could find food and escape from predators. Thus, though always coupled to a particular species, Grinnell defined a niche in terms of ’spaces’ in a community, not in terms of the ’occupants’ of these places (see also Schoener 1989). Therefore, Grinnell’s niche concept allows a niche to be or not to be occupied by a species, and hence that there are empty niches.

To Elton, niches were roles played by species in biocoenoses or ecosystems, a major characteristic being that a particular role (niche) could be played (filled) by several species. Elton was somewhat ambiguous in that on the one hand he spoke of a niche being *filled* by species, while and on the other hand he also saw the *occupants* themselves as a niche: "Or we might take as a niche all the carnivores which prey upon small mammals, and distinguish them from those which prey upon insect" (Elton 1927, p. 64). Mostly, however, he spoke of niches (roles) which could be occupied (fulfilled) by different species. The important aspect of his niche concept is that a niche can be occupied by more than one species. Therefore, more than any other niche concept, Elton’s concept allows there to be empty niches, awaiting, so to speak, to be occupied. Elton’s niche concept is a holistic concept. For that reason, it has become particularly favourite in holistic systems ecology (among others Odum 1963, 1971). The most extreme variant of this niche concept has been formulated by Kroes (1977) who talks of ’primary niches’ being formed by the producing, consuming and reducing components of ecosystems. In this sense, the niche concept becomes equivalent to the concept ’trophic level’. Incidentally, Elton himself laid the foundations for this niche concept: "the niches about which we have been speaking are only smaller subdivisions of the old conceptions of carnivore, herbivore, insectivore, etc." (Elton 1927, p. 64).

Other than Grinnell’s and Elton’s, Hutchinson’s niche concept in the first instance doesn’t allow us to talk of empty niches. For his multidimensional niche is defined by the specific ranges of values of environmental variables allowing *a species* to survive and reproduce. In that sense, each species has its own unique niche. The crucial difference is that Grinnell’s and Elton’s niche concepts are *systems* concepts, whereas Hutchinson’s is a *species* concept. Systems concepts allow there to be empty niches, whereas species concepts don’t. As mentioned, the Hutchinsonian niche may be regarded as a multidimensional *attribute* of a species. In that sense, it is logically impossible to speak of empty niches.

Still, Hutchinson’s niche concept is also somewhat ambiguous in that, once the multidimensional hyperspace forming a species’ fundamental niche has been defined, and especially when it is projected in the concrete space of a certain biotope (Hutchinson 1957, p. 388), the possibility arises to disconnect the ’niche-space’ thus established from the initial fundamental niche of a species. When this is carried through, ’niches’ become ’spaces’ in biotopes again, and we are back at Grinnell’s place niche or habitat niche. The aforementioned definitions by Aarssen (1984) of the Hutchinsonian niche concept are significant in this respect, especially his definition of the available niche of a species: "a real ’place’ (or set of places) in nature (..) [which] is roughly equivalent to habitat" (Aarssen 1984, p. 78). I have argued not for nothing that Hutchinson’s niche concept can be regarded as a precise formulation of the potential habitat of a species.[72] It is probably for this reason that several authors have regarded Hutchinson’s niche concept as a systems concept, with the possibility of empty niches, and not as a species concept (Pianka 1983; Giller 1984; Schmitt 1987). Unfortunately, Hutchinson himself asked "whether the three Nilghiri [species] *fill all the available niches* which in Europe might support perhaps 15 or 20 species, or whether there are really *empty niches*" (Hutchinson 1957, p. 396). I suspect that this was more of a slip of the tongue on the part of Hutchinson, a result of the confusion of different niche concepts to which he was also subjected, rather than that he saw his own niche concept as a systems concept.

Even the resource niche has a certain ambiguity in this respect, though this holds only for the potential niche. For on this concept, too, it is possible, once the set of resources forming

[72]Notice that it is possible to speak of ’empty’ potential habitats (Hutchinson’s fundamental niche, projected in the concrete space of a biotope, and Aarssen’s available niche) but not, of course, of ’empty’ realized habitats.

the potential niche of a species has been determined, and in particular when this set, or a subset of it, has been localized in a biotope, to disconnect it from the initial abstract set of resources defining the potential niche of the species, and to view it as an ’empty niche’ that can be ’occupied’ also by other species. This does not apply, however, to the (0-th, 1-st or S-th partial) realized niche of a species. For this is defined as the set of resources a species actually utilizes. This set can be conceived in two different ways: (1) as the set of resources of which the species (population, individual) actually consumes specific elements, or (2) as the specific set of resource elements which the species (population, individual) actually consumes. In the latter case, every species has, by definition, a unique realized niche, there can be no overlap of realized niches of different species (populations, individuals), and it is impossible to speak of empty niches. In this case the competitive exclusion principle, in the way put by Hutchinson (1957, p. 418), that realized niches do not overlap, would be a tautology. Fortunately, this is not the realized niche concept employed by modern niche theory.

In the former case, in which a species consumes specific elements, that is, a subset, of the set of resources it exploits, there may be other species exploiting the same set of resources but consuming different subsets. This allows different species to have overlapping realized niches. If we let R1 and R2 represent the (S=2-th partial) realized niches of two species, S1 and S2, then R1 is the set of resources species S1 exploits and of which it consumes a subset, say C1, and R2 is the set of resources which species S2 exploits and of which it consumes a subset C2. Though C1 and C2 can never overlap, R1 and R2 may either 1) be completely separate; or 2) overlap; or even 3) be identical. This is the realized niche concept employed in modern niche theory. Since it pertains to specific resource utilization functions of species, there is no need, on this concept, to postulate the existence of empty niches.

On the other hand, this niche concept in no way precludes the possibility of there being (sets of) resources in a biotope which are not (yet) being exploited or utilized by species. That is, it in no way precludes the possibility of there being ’unsaturated’ biotopes.[73]

## 10.4 Habitat differentiation and niche differentiation

In this final section I will draw some conclusions pertaining to the ’principles’ of habitat differentiation and niche differentiation, and the difference between them. Considering the enormous discrepancies in the use of the terms ’habitat’ and ’niche’, these conclusions will be remarkably close to what is commonly held about these ’principles’. I take this to be strong support for the definitions of the terms ’habitat’ and ’niche’ recommended here.

### 10.4.1 Spatial and ’functional’ differentiation

[73]I wouldn’t want to say the same thing about ’incomplete’ ecosystems. I am not a favorite of the use of the terms ’complete’ and ’incomplete’ in this connection, not because there couldn’t be ’unsaturated’ ecosystems (why couldn’t there be?), but because the terms ’complete’ and ’incomplete’ riek too much of essentialistic conceptions of ecosystems. How are we to tell when a system is complete? This is possible only if one has a preconceived idea of what the structure (’nature’) of an ecosystem *should be* like rather than what it is. Should all ecosystems be alike, moreover, or, if not, how many types of systems should there be?

Niche differentiation is generally considered to be the coming into being, in ecological time, of differences in resource utilization patterns between two or more competing species (that is, species having overlapping potential niches), such that in the presence of one another, each species utilizes only a subset of the set of resources which it would utilize if the other were absent. Accordingly, niche differentiation may be defined as reduction of niche overlap such that S-th partial niche overlap is less than 1-st partial niche overlap.[74,75]

At the end of section 10.2.4 I defined habitat differentiation as reduction of habitat overlap such that realized habitat overlap is less than potential habitat overlap. Clearly, however, in dealing with this concept, we will have to make a distinction analogous to the one between 1-st and S-th partial niche, that is, between the 1-st partial (intraspecific) and the S-th partial (interspecific) realized habitat of a species. In other words, habitat differentiation may be more accurately defined as reduction of habitat overlap such that S-th partial habitat overlap is less than 1-st partial habitat overlap.

The major difference between habitat differentiation and niche differentiation is, of course, that the former pertains to spatial separation of species, whereas the latter pertains to so-called 'functional' differentiation, or, better, to diverging patterns of resource use within the same unit of space (that is, within a biotope or within the area of S-th realized habitat overlap).[76] That is, habitat differentiation, if complete, results in non-coexistence, whereas niche differentiation is considered a mechanism of coexistence. We can be a bit more specific, however.

### 10.4.2 Competition, coexistence, and displacement

When comparing the 1-st partial (intraspecific, realized) habitats and niches of two species, S1 and S2, there are three possibilities: S1 and S2 have either (i) separate 1-st partial habitats and separate 1-st partial niches (that is, when experiencing only intraspecific density effects, the species occur in separate sets of environments and they utilize separate sets of resources); or (ii) overlapping 1-st partial habitats and separate 1-st partial niches (they share the same set of environments but utilize different sets of resources); or (iii) overlapping 1-st partial habitats and overlapping 1-st partial niches.[77] Of course, habitat differentiation presupposes

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[74]The relevant parameter to measure niche overlap is niche breadth. See Petraitis (1979) for measures of niche breadth and overlap. See also chapter 11.

[75]Notice that, because niche differentiation pertains to niche overlap, it pertains, by definition, to a relation between (exploitation) competitors. It may be influenced, though, by other factors.

[76]I am not a favourite of the term 'functional' differentiation, because it rieks too much of the functional niche concept and probably also has its origin in that concept. Although niche differentiation is 'functional' for species in the sense that it allows them to coexist, it has nothing to do with 'functions' of species in ecosystems.

[77]It is impossible for different species to have separate 1-st partial habitats but overlapping 1-st partial niches. For the niche of a species is the restriction of its habitat to resources.

1-st partial habitat overlap, and niche differentiation presupposes 1-st partial niche overlap.

It is only when species have overlapping 1-st partial niches (case iii) that (exploitation) competition between them may occur. If so, there are again three possibilities: S1 and S2 have either (1) overlapping S-th partial habitats and overlapping S-th partial niches (that is, they occur in partly the same set of environments and they utilize partly the same set of resources); or (2) overlapping S-th partial habitats and separate S-th partial niches (they occur in partly the same set of environments but utilize different sets of resources); or (3) separate S-th partial habitats and separate S-th partial niches.

In case 1, there are two sub-possibilities: S-th partial niche overlap is either (1a) identical to or (1b) a proper subset of 1-st partial niche overlap. In case 1a, either niche overlap is sufficiently small to allow for coexistence[78] or there must be some mechanism of coexistence other than niche differentiation (for example regulation by another factor than contested resource availability, such as abiotic conditions or a predator, parasite or pathogen). Case 1b may result from niche differentiation, but then the differentiation is incomplete. This may in fact be more likely to occur than case 2, where niche differentiation is complete.

In case 3, there are also two sub-possibilities: S1 and S2 occur either (3a) in the same biotope (requiring that the biotope be heterogeneous) or (3b) in different biotopes. Case 3a may result from niche differentiation, concurring, however, with habitat differentiation. Case 3b may obtain when there are no opportunities for niche differentiation (for instance, because the biotope is completely homogeneous), and when, as a result, one species is competitively displaced by the other. Because in this case S1 and S2's having separate S-th partial niches is a consequence of their having separate S-th partial habitats, this is a case of habitat differentiation, not niche differentiation. (Notice, moreover, that this case results from competitive displacement, whereas niche differentiation is a mechanism of coexistence.)

Three final comments seem to be in order.

Firstly, it depends of course on our definition of coexistence in which of the above cases S1 and S2 may be said to coexist. To coexist may be loosely defined as to occur together in space and time. If we take this to mean that species must occur simultaneously in the same biotope, case 3a would be a case of coexistence. It seems more adequate, however, to apply the term coexistence only to species having overlapping S-th partial habitats, and to hold, more specifically, that it is only within the area of S-th partial habitat overlap that species can be said to coexist.[79] Cases 1a, 1b and 2 pertain to coexistence, then, and cases 3a and 3b to non-coexistence (case 3a has also been referred to as spurious cohabitation (Harper et al.

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When a species has no realized habitat in a particular area, it cannot have a realized niche in that area either. When the realized habitats of different species do not overlap, they can have no overlapping realized niches either. It is possible, however, for different species to have separate realized habitats yet overlapping *potential* niches.

[78]This possibility has lead to the question how different species must be to be able to coexist, or, conversely, how similar they must be not to be able to coexist. This question is known as the problem of limiting similarity (see McArthur and Levins 1967; May 1973, 1981; Abrams 1976, 1983).

[79]Compare this to the definition of a community in the former chapter.

1961) or non-coexistence equilibrium (Braakhekke 1980)).

Secondly, as suggested by the above cases, competition may (but need not) lead to both habitat differentiation and niche differentiation. However, differences in realized habitats or niches may result as well from other processes than competition (for example habitat selection, isolation or predation). Therefore, as noted by Glasser and Price (1982), observations of such differences alone do not permit evaluation of the importance of possible causal mechanisms, and hypotheses about these mechanisms must be tested independently of the observations. Ignorance of this simple methodological rule may not only give rise to a lot of (inconclusive) controversy (see chapter 13) but also block the road to real progress in our understanding of these mechanisms.

Thirdly and finally, niche differentiation may be a sufficient condition for coexistence, but it is not necessary. For "coexisting species can use the same limiting resources [that is, have identical S-th partial niches, RL] by having different per capita effects (..) on any one from j = 1 to T [resources]". This "will occur whenever [their] per capita resource requirements (..) or efficiencies of resource use (..) differ" (Glasser and Price 1982, p. 456; see the next chapter). As noted by Glasser and Price (1982), such differences seem likely, suggesting that the coexistence of competitors may be much more probable than was once imagined. This is particularly relevant to plant species, of course, since all plants require essentially the same resources, whence opportunities for niche differentiation are limited (see also the next chapter).

## 10.5 Conclusions

The purpose of this chapter was to clarify the various concepts of habitat and niche in ecology and to suggest a clear assignment of terms. I have done so by sorting out definitions of these concepts which are separately unambiguous and jointly coherent and consistent. This allowed me to discuss the concepts ('principles') of habitat differentiation and niche differentiation in a way that is strikingly similar (given the ambiguity of the terms 'habitat' and 'niche') to the ecological literature on these concepts. I consider this to be strong support for the definitions as recommended here.

I do not have the pretension that by these definitions the problem of ambiguity of the terms 'habitat' and 'niche' will also be solved in practice and on short notice. The various concepts to which these terms refer have probably struck root too deeply. I'm afraid this applies in particular to the community concept of habitat (H3). I have shown, however, that the problem *can* be solved theoretically, and I can only hope that the conceptual clarifications provided here will be beneficial to the further development and maturation of habitat and niche theory.