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ORIGINAL PAPER

Location and foraging as basis for classification of biotic interactions

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Abstract Ecologists face an overwhelming diversity of ecological relationships in natural communities. In this paper, I propose to differentiate various types of the interspecific relations on the basis of two factors: relative localization and foraging activity of interacting partners. I advocate recognition of four types of environments: internal, surface, proximate external and distant external. Then I distinguish four types of synoikia—one partner lives in different degree of proximity to another; and four types of synmensalism: one partner forages in different degree of proximity to another. Intersection of localization-based (four subtypes of synoikia) and foraging-based (four subtypes of synmensalism) rows results in 16 types of interactions. This scheme can serve as a framework that manages diverse biotic interactions in a standardized way. I have made the first step to set up nomenclature standards for terms describing interspecific interactions and hope that this will facilitate research and communication.

Keywords Interspecific interactions · Synoikia · Synmensalism · Theoretical scheme

Introduction

Interactions among species play a major role in shaping the ecological and evolutionary patterns in natural and human-impacted ecosystems (Wootton 1994; Mougi and Kondoh 2012). The description, analysis, and understanding of biotic interactions are fundamental operations in almost all ecological investigations (Lidicker 1979). Ecologists face an overwhelming diversity of ecological relationships in natural communities, and are trying to integrate many different types of biotic interactions into one theoretical framework (e.g. networks of ecological interactions; Kefi et al. 2015) or build a "periodic table of ecological niches" (Winemiller et al. 2015). The boundaries between different types of biotic interactions are not well defined and often cannot be restricted to distinct categories (Allen and Starr 1982; Parmentier and Michel 2013). These associations are part of a broad continuum in which it is difficult to know where one type of association ends and another begins.

Despite the diverse, uncertain, transitional nature of various interactions, we must know how to distinguish between their various kinds as far as our minds need something stable, rigid, and reliable to work with. Drawing fundamental distinctions between like and unlike entities is an essential step in guiding science and, consequently, is not a job to be taken lightly (Wagman and Miller 2003). Our challenge is to gather and analyse more and better-resolved data to sharpen blurred boundaries and improve predictions. Only by identifying regularities among the phenomena we observe can we hope to uncover the general processes shaping the natural world (Poulin 2007).

Our perception of nature may determine what interactions we find interesting or important (Callaway 2010). Due to practical needs of empirical research specific terms for interaction types routinely observed in nature have been introduced: labels like "synoikia", "epitoikia", "entoikia" emerged (Dogiel 1965), describing interactions with various degree of physical intimacy. There are also: the term "sclerobionts"—all organisms living upon or within any kind of hard substrate, "epicoles"—organisms on any

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more or less hard substrate of organic or inorganic origin, "epizoan"—living organism settling permanently on another living organism (Peel 2014). In some cases it is crucial to discriminate between biotic interactions (live/live interaction) and postmortem encrustation (live/dead interaction) (Gordillo and Archuby 2014). The problem is that such names have no theoretical background: for example, they fell out of scope of the traditional +/0/− outcome-based scheme (Odum 1953) and, consequently, cannot be treated as truly scientific terms (Van der Steen 1990). In many cases, different scientists use the same term to mean different things or different terms to mean the same thing.

What characteristics can we use to categorize various types of interspecific interactions? Different types of relationships between two organisms can be discriminated by, for example, referencing to location, substrate, defense, shelter, transportation, or food. Among these life-sustaining ecological factors I emphasize two: foraging and localization between interacting organisms: where exactly, with respect to the other interacting partner, the routine and foraging activities of organism take place. Arguably, physical closeness of interacting organisms has great impact on the nature of interactions and how we perceive them. For example, many symbionts do indeed exist in very intimate contact, when one organism lives inside, on the surface, or in close proximity to the other partner organism. Foraging ecology is also of unquestionable importance. These two factors constitute a large fraction of biotic interactions.

My goals in this paper are: (a) to circumscribe various forms of direct biotic interactions on the basis of two characteristics: physical closeness of foraging activity and localization of interacting organisms; (b) to construct system of concepts for proposed interaction types with explicit verbal definitions; and (c) to offer names for some of these concepts.

Types of organism's environments

My ecological analysis starts with partner-relevant partitioning of organism's environments. Although the need for formalization and standardization of environment descriptors is growing, and ecologists have put some effort into delimiting the semantic boundaries of overlapping terms (e.g. Niven 1980; Kearney 2006; Buttigieg et al. 2013; Herrando-Perez et al. 2014), the concept "environment" is both vaguely defined and inconsistently used in ecological literature (Alley 1985; Margulis 1990; Wilkinson 2001). This distorts our communication with scientists in other disciplines and alienates general public because we give ambiguous, indefinite, and unstandardized answers to ecological questions in public and legal situations. Similar "semantic disputes" have also occurred in the study of social interactions (e.g. Costa and Fitzgerald 2005) that are but a type of biotic interaction. The word "milieu" may be more appropriate in this context, but the word "environment" has historical priority and, as being broadly used by scientists, is more suitable for this study. An "environment" cannot be described without reference to a particular organism. The term "environment" will be used herein to refer to the space with all the things (living and dead) around and within the target organism.

The major problem is how to demarcate and establish clear definitions for various parts of organisms' environments. Apparently, the partner-related organism's environment can be partitioned in a multitude of ways: it is a typical problem in ecology to define the boundaries for a unit of study (Loehle 1988). One feasible way to operationalize the concept "environment" is to apply the concept "environ" (Borrett and Freeze 2011) or, to divide the organism's environment into direct and indirect parts, to build the so-called "envirogram" (Andrewartha and Birch 1984). Similar work to classify inter-organismal interactions is underway in biological ontologies such as the Population and Community Ontology (Walls et al. 2014). The difficulties of scheme construction are great but not insurmountable (Winemiller et al. 2015). Among tremendous number of combinations of many abiotic and biotic variables I will consider only those that concern only two interacting partners.

I propose to differentiate the space within and around an organism into set of four distinct "environments" where the other partner organism can live (exist, occur) and/or forage. "To live" here means to be physically located, to occupy place, irrespective of any other physiological actions like reproducing or breathing. "To forage" means to search and consume any digestible items. This set includes (verbal form of these concepts are subject for further discussions): (1) internal; (2) surface; (3) proximate external and (4) distant external environments.

The "internal" environment is a space under an organism's boundary (skin, shell, squamae, epidermis, cell membrane for single-celled organism, etc.; epidermic derivates are not included). This definition presupposes that we can unequivocally determine where the border of organism is located in order to say what is inside and what is outside an organism. The interior environment represents the "living milieu", being the most unique and principally different from non-living media like water or air.

The "surface" environment is a surface of an organism's body, including extracorporal entities like spines, tentacles, feathers or hair. It is transitional from internal to external inanimate environment. Strictly speaking, everything that is located outside the surface of an organism is external. But the situation when one partner is in physical contact with the surface of the other is very important ecologically, so I include in this category all cases when the smaller partner locates and/or forages on the surface of the larger partner, including space in/on/between its epidermal derivatives. In this environment two interacting organisms are adjacent to (touching) one another, but not overlapping.

The "external" environment is a zone around an organism. This is a bubble-like volume of space in which the organism is housed. We can take analogy from human psychology, where each person uses verbal and nonverbal clues to establish a surrounding space, a space which has different dimensions and different degrees and types of elasticity in different cultures (Smith and Varzi 2002). This personal space (=external environment) around the human body is carried around with it when the person moves. The size of the external environment greatly varies depending on partner's specific biology and can be specified as touching or visual distance. Any organism—even small in size, or immobile, or with low level of metabolism—changes the properties of the medium in which it lives (Pizzolotto 2009) and, in a sense, creates its environment through its behaviour, morphological and physiological processes (Wright and Jones 2006). For instance, the concentration of nitrogen, oxygen and carbon dioxide surrounding an organism in a burrow is partly a result of its own respiration (Kearney 2006). By the fact of its mere physical presence and physiological activities, an organism possesses the external environment. It partially synonymizes with (1) the behavioural milieu (Umwelt) of a given organism as a set of stimuli that have the value and significance of signals (Canguilhem and Savage 2001); and (2) "limited domain of danger", which represents either a limited detection range or a limited attack range of predators (James et al. 2004). This environment is not monotonous: the nearest surroundings have much greater value for direct interspecific interactions, than distant surroundings.

The part of the environment just around an organism can be named "proximate", that located further—"distant". Sometimes the proximate external environment has sharp rims, i.e. within the boundaries of organism's nest or hole. But more often boundaries are vague, being induced primarily through human demarcation. Proximate external environment is significantly influenced by the organism's own body—physically, chemically and biologically. The distant external environment is effectively out of direct reach of organism: it is "all other" parts of surroundings that scarcely affect organism in the aspect of biotic interactions.

Localization- and foraging-based categories (rows)

Relative to these four environments two conceptual categories (rows) can be formulated. First is a localization-based row: where the dwelling place of one partner, usually a small one (relative to other partner's environment), takes place. Second is a foraging-related row: where the foraging activity of one partner, usually a small one (relative to other partner's environment), takes place. In this paper I consider relatively prolonged interactions, from the "point of view" of the smaller partner. Otherwise, from the viewpoint of the larger partner, we will see predation, filter feeding and other types of "instant" interactions, lethal for the smaller organism.

We can classify interactions from the most intimate (one partner lives and/or forage inside the other—in its internal environment) to the least intimate—distant interactions (one partner lives and/or forage in the distance to another—in its external environment—the cases for remote or indirect interactions) (Fig. 1).

The main obstacle we face here is terminology. Concepts of this area of study still suffer from inconsistencies and confusions over terminology (Costa and Fitzgerald 2005; Kearney 2006). Generally speaking, ecological progress and communication with non-specialists are impeded because many ecological terms have multiple meanings and many ecological terms have meanings similar to each other (Hodges 2008). Only by using precise definitions can we state precise hypotheses (Niven and Liddle, 1994). As theory matures, basic definitions become subject to improvement; the challenge is not to decide which definition has historical priority, but which best promotes further theoretical development. Some terms are already circulating in the biological literature: "ectocommensal" animals (Purcell and Eriksson 2015), "fungal endophytes" (Hamilton and Bauerle 2012), multi-organism processes (Torto-Alalibo et al. 2009).

In the hierarchy of terms describing localization of one partner within environment of another the term "synoikia" (Dogiel 1965) can be considered to be the most general. This term establishes the fact that interacting partners physically locate close to each other (without specifying the degree of intimacy): "*syn*"—together, "*oikos*"—house. Verbal form of this term accurately and precisely discriminates it from the similar term "symbiosis" ("*syn*"—together, "*bios*"—life)—as it is not true living (i.e. full range of living activities) but only housing—cohabitation.

The process of science inevitably involves the introduction of new terms for new concepts. As there are no nomenclature rules for ecological terminology (Herrando-Perez et al. 2014), to name concepts that specify localization of one partner within different environments of

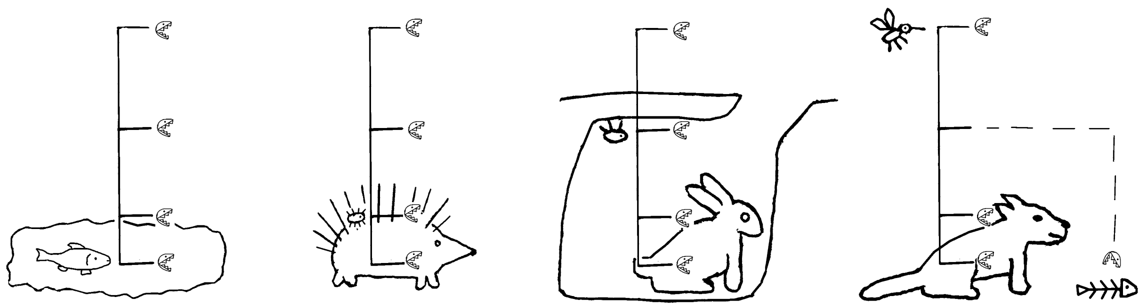


Fig. 1 Illustration of where interacting organisms live (icons of small animals) and forage (nibbler icons) in relation to one another. Four *horizontal lines* (*bottom-up*) correspond to four subtypes of environments: internal, surface, proximate external and distant external. For example, in the *left* part of the figure: a pearlfish lives inside the sea cucumber and forages: within; on the surface; in proximate; and distant external environment

another, I advocate to use four Greek prefixes: "*ento-*", "*epi-*", "*peri-*", and "*ecto-*", corresponding to internal, surface, proximate external and distant external environments. By adding these prefixes to the root word "*oikos*", I construct four localization-based terms: entoikia, epioikia, perioikia, ectoikia. This approach minimizes any addition to existing ecological terminology and incorporates the already existing terms like "synoikia", and "epioikia" into the proposed conceptual framework.

Therefore, definitions of concepts in the localization-based row would be: entoikia for a type of interspecific interaction where one partner lives in the internal environment of another partner (example: pearlfish live, but do not feed, inside the alimentary tract of sea cucumbers); epioikia for a type of interspecific interaction where one partner lives in the surface environment of another (example: certain Goby species live amongst spines of the toxic sea-urchins); perioikia for a type of interspecific interaction where one partner lives in the proximate external environment of another (example: some insects that live in the homes of gophers); ectoikia for a type of interspecific interaction where one partner lives in the distal external environment of another (example: hyenas that follow a lion tribe).

To describe situations when one partner forages in different environments of the other, I use the root word "*mensa*". The term "synmensalism" can be introduced by analogy with the term "synoikia", thus being well motivated in the sense that its exterior verbal form accurately reflects its interior meaning: "*syn*"—together, "*mensa*"—food. It differs from the term "syntrophy", when organisms share a food (Fischbach and Sonnenburg 2011). Synmensalism is a type of interspecific interaction where one partner forages within any environment of the other. It serves as a generic term for more specific interaction types in this foraging-based row. Where exactly partners live does not matter; implicitly places of living and foraging are not the same.

The same Greek prefixes are used: "*ento-*", '*epi-*", "*peri-*", "*ecto-*". By adding them to root word "*mensa*", I construct four types of synmensalism: entomensalism, epimensalism, perimensalism and ectomensalism, which are distinguished on the basis of different localization of partners foraging activity. So definitions of these concepts will be: entomensalism is a type of interspecific interaction where one partner forages in the internal environment of another (example: blood-sucking mosquitoes). This means a consumption of any part of the other partner's body as well as any edible item located within this partner (like its own endosymbionts or earlier swallowed prey). Epimensalism is a type of interspecific interaction where one partner forages in the surface environment of another (example: fish-cleaning species that consume parasites or dead skin particles on the surface of their fish clients); perimensalism is a type of interspecific interaction where one partner forages in the proximal external environment of another (example: scavengers); ectomensalism is a type of interspecific interaction when one partner forages in the distal external environment of another partner (example: heterospecific bird colonies).

I think that these names are more consistent, precise and systemized than similar "entocommensals", "ectocommensalism", "parabiosis" or "epibiontism" (Purcell and Eriksson 2015). Many ecological terms are vague, controversial and inconsistent. The typical examples are terms "commensalism" (Poreau 2014) or "cleptoparasitism" (Breed et al. 2012). Commensalism is a too broad a category, and we have to explicate every time what exactly do we mean by using this term: i.e. "burrow commensalism" (Henmi and Itani 2014). It has many "meanings": broad and narrow, social connotation, microbiological context; it can be behavioural, nutritional, immunological and so on. In the literature we can find terms like "urban commensal rodents" (Garba and Dobigny 2014), "commensal relationship" of house sparrow with humans (Sætre et al. 2012); work interactions between coroners and medical examiners being described as commensalistic (Furness 2012). Like most of such broad categories, it ultimately became unoperational and inconvenient in routine research activities and scientists gradually started to avoid its usage. The term "commensalism" has factually transformed into a terminological cluster of many concepts obscured behind one name. By applying this scheme we can accurately separate and describe interactions that are lumped in such umbrella concepts.

Novel scheme of species interactions

On the crossroads of localization-based rows and foraging-based columns (various categories of synoikia and synmensalism described above) I form a 4 × 4 matrix of 16 possible "topotrophic" types of interspecific interactions (Table 1). Every interaction type can be defined in binominal mode: one characteristic is taken from "*oikos*" row and another from "*mensa*" row: for example, 2A interaction as epioikia/entomensalism; 2B as epioikia/epimensalism.

For all 16 types of interactions we can formulate clear verbal definitions: generic term (interspecific interaction) plus two specific characteristics: localization + foraging. For example, for 3B box we formulate: this is a type of interspecific interaction where one partner lives in proximal external, but forages in surface environment of the other partner, for 2D: this is a type of interspecific interaction where one partner lives in the other partner's surface environment, but forages in the its distal external environment.

Now we should name each interaction type, so that we can talk clearly about them. Some of these terms are already exist (Fig. 2). For example, micropredation for 4A (type of interspecific interaction, where one partner lives in distal external environment of the other and forages in internal environment), inquilinism for 3C (type of interspecific interaction, where one partner lives and forages in proximal external environment of the other). Some terms like ectoparasitism embrace more than one box: 2A and 2B. Other types do not have any specific names yet: in this paper I do not introduce new terms, but think that they could be generated for the purposes of future research.

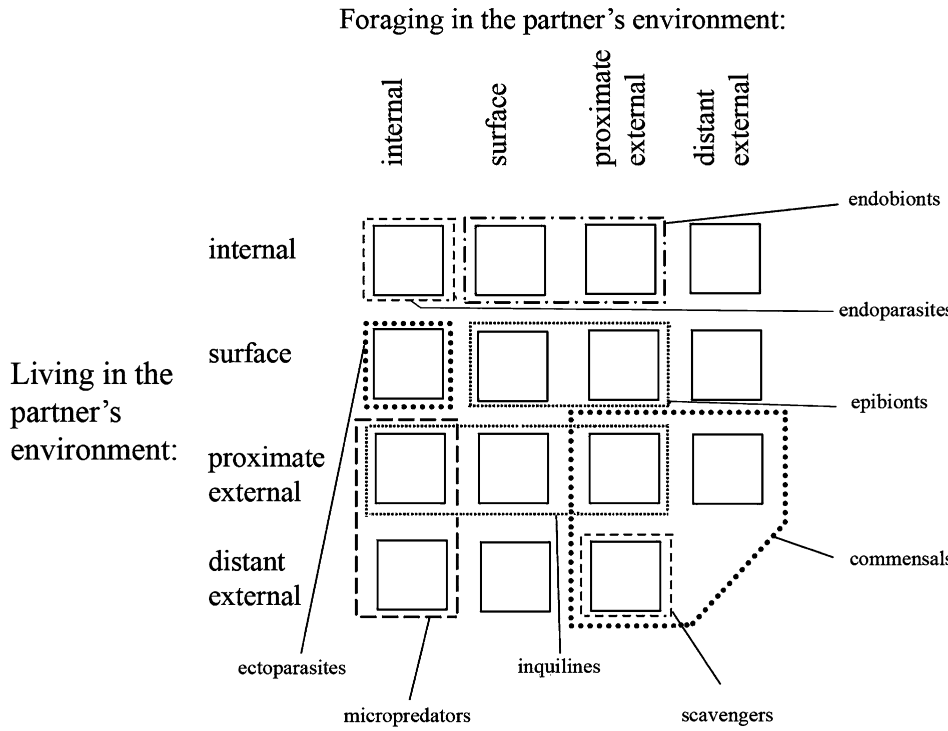
When interacting organisms both forage ("mensa") and live ("oikos") in the same zone, the term "biosis" is applied. For example, terms "epibiont" (Peel 2014)—one partner lives and forages in the surface environment of the other. Parabiosis as a symbiotic association where two species share a nest, forage together, and may even feed each other (Menzel and Blüthgen 2010) = live + forage in the proximal signal environment.

As an example of 4D type (it is a rather theoretical construct to make the scheme complete) can be viewed as the seabirds that forage in the distal signal environment of

Table 1 Examples of interaction types based on locality and foraging activity of partners

Synoikia/ synmensalism	A. Foraging in the partner's inner environment Entomensalism	B. Foraging in the partner's surface environment Epimensalism	C. Foraging in the partner's proximal external environment Perimensalism	D. Foraging in the partner's distal external environment Ectomensalism
1. Living in the partner's inner environment Entoikia	(1A) Gut microbiota	(1B) ??	(1C) Shrimps that live in sea cucumber anuses	(1D) Pearlfish live, but not feed, inside the alimentary tract of sea cucumbers
2. Living in the partner's surface environment Epioikia	(2A) Parasitic plants like mistletoes	(2B) Mallophaga that feed on feathers or hair; epiphytic plants	(2C) Certain goby species live amongst spines of the toxic sea-urchins	(2D) Clownfish that live amongst tentacles of sea anemones
3. Living in the partner's proximal external environment Perioikia	(3A) Bed bug *Cimex lectularius*	(3B) Fish-cleaning species that consume parasites or dead skin particles on the surface of their fish clients	(3C) Some insects that live in the homes of gophers	(3D) Small reptiles in termite mounds
4. Living in the partner's distal external environment Ectoikia	(4A) Blood-sucking mosquitoes	(4B) Oxpecker birds that feed on external parasites of large animals	(4C) Hyenas that follow the lion tribe	(4D) Seabirds that forage in the proximal signal environment of whales or dolphins

Fig. 2 How the traditional terms fit into the proposed scheme



whales or dolphins (Anderwald et al. 2011; Degrati et al. 2014).

To be accurate, type 2B (examples: the Anemone crab lives and captures its food through filtration from within the tentacles of giant anemones; epiphytic plants) is not the same as ectoparasitism and thus allows discrimination between these concepts. 1A (type of interspecific interaction, where one partner lives and forages in the internal environment of the other) is broader than endoparasitism, as it includes also harmless and mutualistic endosymbionts.

From this theoretical perspective, we can sharpen the concept "symbiosis". Symbiosis is often described by physical attachment of organisms of different species—the so-called "conjunctive symbiosis" (Margulis 1990). In our scheme, symbiosis (in its strict sense) can be defined as any interaction where one organism lives within the internal or surface environment of the other.

All these interaction types can fluctuate between mutualism, commensalism, and parasitism: for example, parabiosis (Menzel et al. 2014); as far as they are independent from the outcome-based scheme.

Conclusion

To sum up, this communication proposes a new classification scheme, which simply and comprehensively illustrates relationships between the various kinds of associations. Obviously, not all interactions will neatly fit into this scheme: "as always with classifications of nature, it is easy to find exceptions; the real challenge, the constructive work, is not to find the exception, but to use this to improve, modify or even change the general framework" (Southwood 1977, P. 338).

This scheme can serve as a framework that manages unpredictable, chaotic or erratic biotic interactions in a standardized way. The scheme has biological sense, relying on such basic ecological characteristics as localization and foraging. This system is inherently complete: any interaction which occurs between two organisms can be unambiguously assigned to a particular category. The proposed framework unifies the conceptual formulation and forms the basis of terminological development: if the terminology proposed here is used consistently, there will be less confusion about what is implied than with the current overlapping, inexact usage.

I have elaborated this classification to be coherent and logically consistent. It is relatively simple and can explain, define and name interaction types that are not covered by other frameworks. The scheme allows justifying newly introduced terms like synmensalism and its subtypes. This approach might enhance cross-data comparisons and meta-analytical efforts in biotic-interaction research (Poelen et al. 2014), with the support of available ontologies (Smith et al. 2005).

This framework can also be used as a teaching tool, moving the teaching of biology beyond the transference of a vast compendium of facts. This scheme organizes scattered empirical facts into a single body of knowledge and arranges data in a logical manner suitable for easy presentation and comprehension.

We must take the challenge to standardize terminology seriously, so that we can make meaningful statements to advance science. I have made the first step to set up nomenclature standards for terms describing interspecific interactions and hope that this will facilitate research and communication. I hope that this communication could be a starting point for future discussions.

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