Hidden values in competing concepts of community-level biodiversity

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1 Introduction

Biodiversity is an ambiguous concept. Its basic ambiguities result from the circumstance that it is a so-called thick concept that inherently links both facts and values (cf. Takacs 1996, Callicott et al. 1999, Kirchhoff/Trepl 2001, Sarkar 2005, Potthast 2007). The evaluative component often remains implicit and unreflected as is evidenced by the frequent talk of *the* biodiversity which ignores that any meaningful concept of biodiversity – be it at the genetic, species or community level – necessarily includes criteria to determine which of the open-ended differences among biological entities shall be relevant or irrelevant. Secondary ambiguities result from the coexistence of different perspectives on biodiversity, e.g. taxonomic versus functional (cf. Callicott et al. 1999), and of different values of biodiversity, e.g. instrumental and eudaemonistic values (cf. Krebs 1999, Sarkar 2005, Kirchhoff 2012, Sandler 2012). These ambiguities are frequently leading to misunderstandings and valuation discrepancies in discourses on biodiversity.

This paper is concerned with community-level biodiversity which comprises within-community diversity and between-communities diversity at different scales. For many reasons the assessment of community diversity is more difficult than that of species or genetic diversity. That is mainly because the objects are still less unambiguously defined at this level than at the two other levels: There is a multitude of competing concepts which define, characterize and delineate ecological communities in quite different ways; and even under one definition, ecological

communities can hardly be delimited unambiguously (cf. Jax 2006, and also Whittaker 1962, Kirchhoff 2007). I will not delve here into the details of the classification and delineation of ecological communities or of the measurement and evaluation of community-level biodiversity. Rather, I would like to demonstrate a fundamental opposition within the discussion about the nature of ecological communities which causes basic conceptual, semantic and evaluative differences as regards community-level biodiversity.[1] First, I characterize two currently influential concepts of the organization of ecological communities and propose a corresponding distinction of two concepts of community-level biodiversity. Second, I illustrate that these concepts imply opposing evaluations of anthropogenic changes of community-level biodiversity. Third, I propose an explanation for the existence and persistence of these competing concepts that highlights the influence of culturally shaped patterns of interpretation on the formation of ecological concepts. I conclude with two summarizing and two subsequent theses.

2 Competing concepts of ecological communities and opposing concepts of biodiversity

Since the very beginnings, the science of ecology is driven by fundamental controversies about the causes of species distributions, the character of the interrelations among coexisting species, and the ontological status of the ecological communities or ecosystems that ecologists distinguish in their classifications (Hubbell 2001, Jax 2006, Kirchhoff 2007, Kirchhoff/Voigt 2010). The classical controversy is that between organismic holism and elementaristic individualism. The former conceives of the relationships among the species of an ecological community in analogy to the relations among the organs of an individual organism,[2] the later regards the distribution of species as largely independent from one another so that species form nothing but loose assemblages.[3] For quite some time, most ecologists have dismissed both of these extreme views (cf. Price 1999: 433), while organismic concepts are still quite influential in lifeworldly views of nature, nature conservation, and some schools of environmental management.[4] In ecology, instead a real plethora of intermediate concepts has been formulated. Nevertheless, a fundamental borderline still exists between two competing concepts that I call *idiosyncratic interactionism* and *generic interactionism*. Both emphasize the influence of biotic interactions on community organization, differ, however, as regards the character of these in-

[1] For an overlapping, insightful approach to clarify concepts of community-level biodiversity see Maclaurin/Sterelny 2008: 106-131.

[2] Classical representatives of this view are A. F. Thienemann and E. P. Odum (Kirchhoff 2007: 205-233). F. E. Clements, contrary to the conventional interpretation, does not hold an organicism in the specified sense but a deterministic theory of competition hierarchies (ibid.: 169-186).

[3] A classical representative of this view is H. A. Gleason; recent exponents are Hengeveld and Walter (Kirchhoff 2007: 187-204, 322-327).

[4] One prominent example is the Resilience Alliance (see Kirchhoff et al. 2010).

teractions. Based on Max Weber's (1904/1949) sociological method, I characterize these concepts in an idealized way, that is, for heuristic reasons I one-sidedly enhance selected aspects to uncover the peculiarities of alternative concepts.[5]

2.1 'Idiosyncratic interactionism' and 'biodiversity as mosaic of coevolved local uniqueness'

The basic assumption of idiosyncratic interactionism[6] is that ecological communities, if they have been able to develop undisturbed, consist of species that have accomplished a shared evolutionary history. During this common history, the coexisting species have adapted to one another by one-sided and mutual, coevolutionary processes of natural selection and now display unique traits that reflect these adaptations. Niche specialization and co-speciation have led to maximal internal differentiation. Specialized trophic interactions and phenomena like compensated trait loss[7] have evolved that tightly interlink the species. In this way, nearly everywhere in the world unique ecological communities with a characteristic species composition, many endemic species, and idiosyncratic ecological interactions have developed. The ecological communities as a whole have adapted to their respective habitat and, at the same time, have changed their habitat such that both, ecological community and habitat, together form a superordinate unity: a stable ecosystem that represents a natural unity of the biosphere (which is able to adapt itself to slight modification of its environment). The biosphere, naturally, consists of a manifoldness of such unique local ecosystems. These are regarded either as largely independent from one another or, usually, as subsystems of an all-embracing global ecosystem.

Idiosyncratic interactionism is confronted with the objection that many local ecosystems have many species in common. This objection is rejected by an additional hypothesis about intraspecific differentiation: The different local populations of these common species differ in their *geno*type and consequently in their phenotype because they are adapted to the particular conditions of their local ecosystem (see Thompson 2005: 7/365 f., Pennisi 2012).

I propose to call the concept of biodiversity that corresponds to idiosyncratic interactionism '*biodiversity as mosaic of coevolved local uniqueness*'. This concept determines basic assumptions as regards the evaluation of both dimensions of community-level biodiversity: within-community diversity and between-communities diversity. That is so because this concept defines how community-level biodiversity naturally organizes itself and, thereby, sets a reference for the evaluation of stocks of and changes in community-level biodiversity.

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[5] See for this method Hekman 1983, Hirsch Hadorn 1997, Kirchhoff 2007: 58-62.

[6] I have built this ideal type especially on Abrams 2000, Angermeier/Karr 1994, Ehrlich/Raven 1964, MacArthur 1972, J. Thompson 1994, 2005, 2009, Traveset/Richardson 2006.

[7] Compensated trait loss is a loss of a physiological ability of a species that is compensated by its interactions with other species (Ellers et al. 2012).

2.2 'Generic interactionism' and 'biodiversity as structured continuum of assembled local differences'

Generic interactionism[8] shares with idiosyncratic interactionism the assumption that the selection of species of the regional species pool by abiotic and biotic factors, so-called abiotic and biotic filtering, is a central principle of the organization of local ecological communities. Contrary to the concept of shared evolutionary history, however, it is assumed that a major part of the earth's surface is occupied mainly by organisms that are rich in ecological interactions with one another but have had no detailed evolution history with one another (Janzen 1985: 309). The basic principle of community organization is not local coevolutionary adaptation but "ecological fitting" (ibid.). '*Ecological fitting*' means that species get together that fit together as regards their abiotic and biotic requirements and tolerances but have evolved the relevant suite of traits independently from one another, elsewhere under different environmental conditions. When species come into a new setting of ecological interactions, they exhibit so-called phylogenetic niche conservatism and preadaptations[9] to the novel conditions: if environmental conditions change, the adaptive traits of the species remain unchanged and the species survive by immigrating into areas that now display conditions that fit to their old adaptations. Ecological succession is not regarded as a process of an increasingly tighter integration of an ecological community but as a process in which species individually colonize suitable habitats and individually react to the omnipresent changes of the environmental conditions. The biosphere is considered not as a manifoldness of tightly integrated, unique local ecosystems but as a fluctuating, flexible web of interacting species. Within this web ecosystems can be delineated arbitrarily only, that means as artificial unities according to criteria selected according to interests.

The concept of ecological fitting presupposes that ecological interactions have rather generic than idiosyncratic character so that – in most cases – several species are more or less ecologically equivalent and thus interchangeable; namely, polyphagous generalists outweigh oligophagous and monophageous specialists.[10] This is assumed to hold true even for most trophic interactions in complex food webs, in some cases indeed for parasitism that is traditionally considered an obligate interaction. The assumption of generic interactions is qualified, however not suspended, by an emphasis on phenotypic plasticity that allows for short-term *onto*genetic adaptations and niche shifts independently from a shared evolutionary history of genotypes; thus, many organisms are quite flexible as regards their capabilities of interactions.[11]

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[8] I have built this ideal type especially on Agosta 2006, Agosta et al. 2010, Agosta/Klemens 2008, Harvey et al. 2012, Hubbell 2001, 2005, Janzen 1985, Wilkinson 2004, Zamora 2000.

[9] For this hypothesis see especially Agosta et al. 2010, Wiens et al. 2010.

[10] Hubbell's (2001, 2005) neutral theory is an extreme version of this view (Kirchhoff 2007: 328-357).

[11] For this paragraph see especially Agosta et al. 2010, Agosta/Klemens 2008, Harvey et al. 2012.

Generic interactionism is confronted with the objections that (i) competition prevents the coexistence of ecologically equivalent species and (ii) coexisting species always enter into coevolutionary interactions that lead to evolutionary divergence and specializations. Objection (i) is countered by the argument that competitive exclusion is rare, for example because competition is often low as densities of competing populations are often diminished by adverse environmental conditions and because inversions often occur within the competitive rank order grace to fluctuations in abiotic conditions or in complex competition systems even under constant abiotic conditions.[12] Objection (ii) is answered by a theory of convergent evolution:[13] A shared evolutionary history frequently does *not* lead to specialization because (a) every species has to adapt itself to many different species at the same time, (b) this set of species is permanently fluctuating as the environmental conditions permanently change, and (c) this set is different for every local population of a species whereby the local populations of this species are interlinked by gene flow so that they cannot adapt independently from one another to the specific local conditions of their habitat. Consequently, many species in many cases adapt themselves to average conditions of their biotic environment, so that functionally more or less equivalent species arise.

I propose to call the concept of biodiversity that corresponds to generic interactionism '*biodiversity as structured continuum of assembled local differences*'. This concept determines basic assumptions as regards the nature of both dimensions of community-level biodiversity that are quite different from those set by the concept of 'biodiversity as mosaic of coevolved local uniqueness'.

3 Practical implications: opposing evaluations of neobiota

Idiosyncratic and generic interactionism just as the corresponding concepts of biodiversity differ fundamentally as concerns the evaluation of anthropogenic modifications of the biosphere. I highlight main differences by reference to the longstanding debate about anthropogenic introductions of neobiota[14] (Richardson 2011) that are often pejoratively called anthropogenic biological invasions.[15] Analogous differences could be demonstrated as regards, example given, the consequences of climate change or the possibilities and limitations of human construction of novel ecosystems.

[12] For classical texts on these arguments see Kirchhoff 2007: 295-304, 315-322.

[13] See especially Harvey et al. 2012, Hubbell 2001, 2005, Zamora 2000.

[14] Neobiota are organisms that – assisted by human agency or not – have for the first time established in a region. I do not distinguish here archaeobiota (established before 1492) from neobiota (established after 1492).

[15] For the cultural background of this debate that explains its frequent vehemence see Eser 1999, Kirchhoff/Trepl 2001, Coates 2006, Kirchhoff/Haider 2009.

3.1 Neobiota are generally problematic

In this debate one group of authors[16] states that the current anthropogenic introductions differ not only quantitatively as regards frequency, species numbers and migration distances, but also qualitatively as regards effects from the historic natural and historic anthropogenic introductions. While the relatively few historic neobiota could be integrated into the historically developed local ecosystems of native species, the numerous current neobiota cannot; instead, they corrupt the organization of the native ecological communities where the neobiota tend to dominate as they frequently have no specialized enemies in their new habitat.[17] One speaks of "Nature Out of Place" and bewails "an unending stream of invasions [that] is changing … ecosystems from productive, tightly integrated webs of native species to loose assemblages of stressed native species and aggressive invaders" (van Driesche/van Driesche 2004: 2). The current anthropogenic stream of neobiota is regarded as *generally* problematic as it overrides the natural principles of ecological organization that would lead to tightly integrated ecosystems of coevolved species. Some authors conclude that neobiota should be excluded from the definition of biodiversity (e.g. Angermeier 1994).

Such an evaluation of neobiota is implied by 'idiosyncratic interactionism' and the concept of 'biodiversity as mosaic of coevolved local uniqueness'.

3.2 Neobiota can be both: harmful or useful

A second group of authors[18] admits that the current anthropogenic introductions differ quantitatively from historic natural and anthropogenic introductions, but dispute that they have qualitatively different consequences. These authors emphasize the dynamic character of ecosystems, point to extensive historic introductions of neobiota and argue that foreign species do not differ significantly from native species as regards the great majority of ecological interactions. Some authors even question the distinction between foreign and native species arguing that all species at any time of their history have immigrated into new areas. This is not to deny that *some* neobiota have undesirable effects; but it is refuted that neobiota are mostly harmful because of a systematic reason, namely lack of coevolution. Some authors instead regard neobiota as enrichment because they increase species numbers at regional and local scales, and thus the spectrum of ecological guilds,[19] and thus

[16] See, e.g., Angermeier 1994, Cassey et al. 2005, Sala et al. 2000, Simberloff 2005, van Driesche/van Driesche 2004.

[17] For a discussion of this enemy release-hypothesis see Chun et al. 2010.

[18] See, e.g., Brown/Sax 2004, Davis et al. 2011, Sagoff 2005, Sax/Gaines 2003, K. Thompson et al. 1995, Walther et al. 2009.

[19] An ecological guild is a group of species that have similar requirements and play a similar role within a community (even though they may belong to quite different taxa).

the probability of complementarity and sampling effects that improve the allocation of resources.[20]

Such an evaluation of neobiota is implied by 'generic interactionism' and the concept of 'biodiversity as structured continuum of assembled local differences'.

4 Cultural background of the opposing concepts

Up to this point, I have characterized opposing concepts of ecological communities and biodiversity, and I have touched on their opposing practical implications. Now I change to a meta-theoretical perspective and propose an explanation for the existence of these oppositions that highlights the influence of culturally shaped patterns of interpretation on views of nature. My hypothesis is that these opposing views of nature are inspired by opposing ideals of human individuality or society respectively that are projected onto nature (cf. Trepl 1994, Eisel 2004, Kirchhoff 2007, Voigt 2009, Kirchhoff et al. 2012a).

I skip the general epistemological justification of this hypothesis that would refer to the findings of anti-positivistic philosophy of science and historical epistemology (see Kirchhoff 2007: 27-55, Kirchhoff et al. 2012a, and the literature cited there), and directly substantiate it based on one of the two views of nature: namely 'idiosyncratic interactionism' and the concept of 'biodiversity as mosaic of co-evolved local uniqueness'. This concept of biodiversity might (in the context of nature conservation, landscape planning, etc.) in most cases be meant if one speaks – without attributive determination – of the maintenance of *the* biodiversity. My specific hypothesis is that this view basically represents a reformulation of Herder's theory of culture. To support this interpretation, I first outline Herder's theory of culture to show that these views of nature are structurally analogous to this theory of culture. Similar isomorphies could be demonstrated with Durkheim's (1893/1933) theory of organic solidarity. Second, I point to the historic influence of Herder's theory on ecology.

4.1 Herder's theory of cultural uniqueness

About 1800, Johann Gottfried Herder has developed a philosophy of history that criticizes all enlightenment's philosophies of history, especially the enlightenment's universalism and ideas of freedom. The aim of human history, according to Herder, is *not* to eliminate cultural differences and to construct societies everywhere in the world in the same way according to allegedly ahistorical universal principles. Rather, everywhere in the world unique cultures shall emerge as the result of an organic development that is guided by two interdependent principles: namely by the particular character of a people and by the particular natural condi-

[20] For theories on these effects see Hector et al. 2002, Tilman et al. 1997.

tions of its place of living (Herder SW: especially IV/204 f., V/509, VIII/210, XIII/253-318, 347-349, 363, 370, XIV/38, XVII/287).[21] Cultural development succeeds if the people gently uses and thereby shapes its place of living according to the latter's natural conditions and to its own particular character; that is the people develops unique forms of land use, housing, social organization etc., thereby detaches itself from direct environmental constraints, and thereby stabilizes favorable environmental conditions – without eliminating the particular character of its place of living. At the same time, the particular environmental conditions of the place of living shape the people's sensibility, language and way of thinking, and thus influence the character of the people's cultural achievements. As regards the people's individuals, Herder holds that each of them is required to develop its particular natural talents with regard to the particular environmental conditions and to the particular organization so far gained by the people (ibid.: XIII/291, XVII/122, XVIII/308 f.). The overall result of this organic development is a harmonic regional unity of a people and its place of living. This unity has a unique character and exhibits a characteristic diversity of cultural achievements that encompasses both a divers unique cultural landscape and a divers unique regime of customs, folksongs, poems, stories etc.; "it belongs to the perfection of human nature to organize and shape itself anew under every sky [here meaning: climate], in every age, and every peculiar mode of existence" (ibid.: XII/8, my translation). If this happens everywhere on Earth, a manifoldness of unique cultures emerges. Each has its principle of perfection in itself, each has to be respected for its own sake – and each has to be preserved from homogenization.

I hope this short description has made visible that 'idiosyncratic interactionism' and the concept of 'biodiversity as mosaic of coevolved local uniqueness' show a structural analogy to Herder's theory of culture: namely, the ecological community corresponds to the people, the superordinate unity of ecological community and habitat to the superordinate unity of people and place of living; and in both theories it is assumed that unique historic processes lead to unique, differentiated unities.

4.2 Herder's theory of culture, geography and ecology

In pointing to this structural analogy, I do not claim a direct influence of Herder's theory on ecology. Rather, the influence has been indirect, mediated by geography (see for the following paragraph Trepl 1987: 103-138, Trepl 1997, Kirchhoff 2007: 487-497, Kirchhoff/Trepl 2009, Kirchhoff et al. 2012a).

Idiosyncratic interactionism stands in the tradition of holistic ecology. Holistic ecology did not arise in the frame of biology but at the intersection of organismic biology and classical geography. Now, the research program of classical geography was in fact based on Herder's theory of culture – an influence that has been admit-

[21] For the following interpretation cf. Eisel 1980, 1992, Spencer 1996, Kirchhoff 2005.

ted by its founder, the German Carl Ritter, and reconstructed by studies in the history of geography (Glacken 1973, Eisel 1980), so that "one could maintain that modern cultural geography started with him [Herder]" (Glacken 1973: 129). This influence is obvious in the fact that classical geography interprets landscapes as objectively given physiognomic unities and 'spatial individuals' that arise and gain uniqueness in a process of organic interaction between cultural and physical factors, or people and land.[22] The research program of classical geography became influential all over Europe, and in the USA as well (Martin 2005: especially 107-128, 141-143, 305). On this background, holistic ecology emerged about 1900 when (i) the physiognomic, that is *aesthetic*, vegetation unities so far described in phytogeography were reinterpreted as *causal*, *functional* unities of interacting species and, at the same time, (ii) these functional unities were interpreted as spatial individuals according to the research program of classical geography.

5 Conclusion

To conclude my analysis, I set up two summarizing and two subsequent theses:

(1) The current discourses on biodiversity feature a fundamental opposition between two concepts of community-level biodiversity that often remains unreflected: a concept of 'biodiversity as mosaic of coevolved local uniqueness' faces a concept of 'biodiversity as structured continuum of assembled local differences'.

(2) On the one hand, these opposing concepts correspond to opposing scientific concepts of ecological communities: namely 'idiosyncratic interactionism' and 'generic interactionism'. On the other hand, these opposing concepts of biodiversity – as well as the corresponding scientific concepts of ecological communities – include hidden values in that they are inspired by opposing ideals of human individuality or society respectively. The former concepts of biodiversity and ecological communities respectively are *structurally* conservative (as it is supported by the presented structural analogy and historical connection with Herder's theories); the latter concepts are structurally progressive (what could be substantiated by revealing their structural analogies with progressive concepts of human society and individuality[23]). By the example of the evaluation of neobiota I have shown how the opposing concepts lead to quite different practical implications.

(3) Current discourses on environmental management exhibit a strong trend to justify the aim to maintain historically shaped local biodiversity by reference to its instrumental value arguing – according to the concept of 'biodiversity as mosaic of

[22] For the underlying concept of landscape, its critique and alternative concepts see Kirchhoff/Trepl 2009, Kirchhoff et al. 2012b, and the literature cited therein.

[23] This reconstruction could start from the Enlightenment concepts of individuality, society, and human history that Herder criticized, namely liberalism and democratism (see Voigt 2009, Trepl/Kirchhoff 2013) but would additionally have to lean on more recent characterizations of modern societies and economies that reflect phenomena like globalization, universalism, institutional/technological isomorphism, product substitutability, and flexibilization.

coevolved local uniqueness' – that the maintenance of this biodiversity is the prerequisite for the maintenance of ecosystem integrity or ecosystem functioning,[24] and, thus, of sustainable ecosystem services for humans. There is, however, considerable evidence that this view represents a doubtful reinterpretation of historically shaped unique landscapes, that are basically aesthetic unites, as functional, ecological unities (Cosgrove 1984, Trepl 1997, Kirchhoff/Trepl 2009, Kirchhoff et al. 2012a, Kirchhoff et al. 2012b).

(4) This assessment is *not* a plea to abandon the protection of historically shaped local biodiversity. Rather, it is a plea to embed this aim into the aim to protect unique cultural and natural landscapes because of their ample eudaemonistic values that involve scenic beauty, symbolic meanings, emotional attachments, and sense of place. But it is a plea against the strong trend to treat cultural values of nature within the framework of ecosystem services (cf. Kirchhoff 2012).[25]

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[24] For a distinction of concepts of ecosystem functioning see Jax 2010.

[25] I would like to thank both reviewers for their helpful comments.

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