Ecological Complexity xxx (2012) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Research Article

Functional complexity: The source of value in biodiversity

Keith D. Farnsworth *, Olga Lyashevska, Tak Fung

School of Biological Sciences, Queen's University Belfast, Belfast BT9 7BL, UK

ARTICLE INFO

Article history:
Received 5 January 2011
Received in revised form 6 February 2012
Accepted 6 February 2012
Available online xxx

Keywords:
Economic value
Ecological economics
Food-web
Functional information
Information theory
Instrumental value
Noah's Ark problem
Phylogenetics

ABSTRACT

Biodiversity may be seen as a scientific measure of the complexity of a biological system, implying an information basis. Complexity cannot be directly valued, so economists have tried to define the services it provides, though often just valuing the services of 'key' species. Here we provide a new definition of biodiversity as a measure of functional information, arguing that complexity embodies meaningful information as Gregory Bateson defined it. We argue that functional information content (FIC) is the potentially valuable component of total (algorithmic) information content (AIC), as it alone determines biological fitness and supports ecosystem services. Inspired by recent extensions to the Noah's Ark problem, we show how FIC/AIC can be calculated to measure the degree of substitutability within an ecological community. Establishing substitutability is an essential foundation for valuation. From it, we derive a way to rank whole communities by Indirect Use Value, through quantifying the relation between system complexity and the production rate of ecosystem services. Understanding biodiversity as information evidently serves as a practical interface between economics and ecological science.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Great concern over biodiversity loss has stimulated efforts to quantify its value, but these efforts have been impeded by difficulties over the definitions of both biodiversity and value, leading to a wide range of concepts, methods and outcomes. Our aim here is to develop a scientifically based measure of the value of biodiversity, having defined it literally as the diversity (i.e. degree of difference) in a biological system. This measure will be based on an estimate of the complexity of the biological system, which we equate with its functional information content, and that we separate into genetic (sub-organism level) and ecological (super-organism level) complexity, following an empirical analysis presented in Lyashevska and Farnsworth (2012). This treatment gives a formal and precise meaning to biodiversity that rests on information theory and recognises biodiversity to be fundamentally a measure of ecological complexity.

De Groot et al. (2010) and Nunes and van den Bergh (2001) reviewed economic approaches to valuing biodiversity and its ecological consequences, showing that economists mainly value the services that biodiversity hypothetically provides to humanity, rather than attempting to value biodiversity itself. This implies that the complexity, which biodiversity measures, can be substituted by another source of its services, following the key assumption of neo-classical economics that consumers are to maximise their utility whilst remaining indifferent as to its source. Both philosophical and instrumental objections to that assumption were identified by Spangenberg and Settele (2010) in relation to ecosystem services.

The obvious response is to attempt to estimate the value of biodiversity in and of itself, directly. Here we propose that this difficult task becomes possible when the closely linked concepts of information and complexity unify all the stages between measuring biodiversity and quantifying instrumental (use and indirect-use) value. Thus, we explore the construction of an information-based measure of value, linking the natural science tradition and that of economics through information concepts. For this, we compose a precise definition of biodiversity in terms of information, especially functional information, which we seek to quantify using ideas developed mainly from genomics and information theory, applying these to levels of organisation from the gene to the ecological community. We then consider the function of biological information, identifying 'functional information' as the source of a 'natural utility': the propensity to increase biological fitness. Information theoretic metrics are then combined with the economic concept of 'ecological importance' introduced by Perry (2010), leading to measures of indirect use value for biological complexity which we argue is what biodiversity estimates. It should be noted that here we are exclusively concerned with objective valuation, so do not include subjective, e.g. existence, value in our analysis; we also exclude direct use-value since there are simpler economic methods for its

* Corresponding author.
E-mail address: k.farnsworth@qub.ac.uk (K.D. Farnsworth).

1476-945X/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecocom.2012.02.001

estimation. Thus our focus is on deriving indirect-use value from biodiversity.

2. What (really) is biodiversity?

Hitherto, there has been no agreed definition of biodiversity which is both precise and comprehensive (see e.g. Norton, 1994; Purvis and Hector, 2000; Ricotta, 2005; Mooers, 2007).

Our starting point is to identify biodiversity with information. The word 'biodiversity' literally means the diversity within a biological system, where diversity quantifies the total difference among the system's parts. This definition coincides with the 'diaphoric definition of data' (Floridi, 2003, 2005), in which a binary (Boolean) bit is the unit of data and a bit is a single difference in any system. In this context, data is the natural pattern of difference which gives form to the system, not a recording of information obtained from it. If (a) biodiversity is the measure of total difference, and (b) difference is data, then biodiversity is properly a measure of the formative data content *instantiated by* a biological system. Analysis of data content is the subject of information theory in the classic interpretation of data as information, but information has many meanings, requiring very precise definition for our progress (Floridi, 2003).

A connection between biodiversity and information is now well established in the form of various indices of biodiversity inspired by the communications theory of Shannon (1948). Pioneering authors regarded biodiversity as the measure of information contained in an assembly of organisms (see e.g. Margalef, 1958), this information being the raw material (i.e. data) for ecological study. Biodiversity indices would quantify the information yield, but crucially, this meant information *about* the system, or a sample of it, not the information *embodied within* the system. The value obtained would depend on sample size, sampling effort and the arbitrary choice of categorising level (e.g. species, genes, or higher order systems): it described the information perceived by the observer. There is very much more information present in a biological system than can be counted by simple observation, so its quantification via counting species or even genes amounts to gross bias by discarding. As well as missing a great deal of the information present, biodiversity indices based on such observations may be sensitive to information that has no functional significance. This is especially the case in recording abundances, because particular abundances in a sample are only 'snap-shots' of constantly changing variables, taken at an arbitrary time Magurran and Dornelas (2010). System-level information is held in the relationships governing these variables, not a set of their values at any particular time. Again, the problem can be identified as one of registering information about the system, rather than within it. The information within the system is the form of relationships among its components, not a transitory count of these components. The value of a biological system is not to be found in a measure of its diversity, but rather in the diversity itself.

2.1. Biological systems as information

Some, but not all of the embodied information is 'effective' in the sense that it can cause a predictable change in a system. MacKay (1969) referred to information as 'a distinction that makes a difference' and later Bateson (1972) more famously called information 'a difference that makes a difference'. In both these statements, information is defined through its interaction with the physical world to create a predictable (i.e. non-random) effect. To avoid confusion with definitions in Shannon's information theory or semiotics, we call this information that makes a difference *effective information*. This concept enables us to distinguish between functionally significant and random information, with a view to isolating the former in biodiversity measures. The justification for that is that information which makes no difference, by definition contributes nothing to instrumental value. The two categories, effective and random information, coincide with Gell-Mann and Lloyd (1996, 2003) terms: 'regularity' and 'randomness', where only regularity is functional. Thus we seek to isolate and quantify only the effective information content of the system. Let us then classify the total information content of any system by two distinct components: $I_{tot} = I_E + I_R$, where I_E is the pattern-forming effective information and I_R is the entropic, random information. Each of these terms can be quantified by the algorithmic information content (Chaitin, 1990) if the term can be isolated. I_E could, in principle, be quantified by the Gell-Mann and Lloyd (1996, 2003) 'Effective Complexity', defined as the minimum description length of regularities, but only given prior information about the regularities (see McAllister, 2003, for an expansion of this criticism). We are searching for a way to identify I_E without such prior information.

Bates (2005), quoting earlier works, defines information as: 'the pattern of organization of matter and energy'. This definition peculiarly addresses effective information. Patterns show either order (characterised by symmetry) or complexity (broken symmetry). Crystal lattices and DNA provide concrete examples of these two kinds of pattern. Schrödinger (1944) realised that symmetrical order was insufficient to account for the genetic information coding life, concluding that it must be in some aperiodic (non-symmetrical) molecule (well before the discovery of DNA). The broken symmetry which generates the organised aperiodicity required to store large quantities of effective information is found in a 'complex system'. Adami et al. (2000) subsequently showed how all biological systems are complex systems in this scientific sense. Thus, we are looking to distinguish complexity from its accompanying random information, within the algorithmic information content (AIC), embodied in a biological system. Using Bates' (2005) definition, we count biocomplexity (complex pattern) as the storage of effective information in nature and set this as the target for biodiversity measurement.

Biological complexity exists within a set of hierarchical levels (see Table 1) and is added to by interactions among them. This modular hierarchical structure means that biodiversity includes the diversity of: molecular structures; networks and pathways (responsible for processes such as metabolism and protein synthesis); cell types; tissues and organs as well as whole organisms and the way they interact in community networks (note: Sarkar, 2002, argued that including all this amounts to biodiversity becoming all of life, including its behaviours). One of the key properties of these hierarchies is self-organisation and emergent complexity – the spontaneous creation of effective information from complex order (Adami et al., 2000). Hierarchical

Table 1
A nine-level hierarchy of biocomplexity. Left column names the level of organisation and right column gives examples of the complex interactions and processes that take place at that level, contributing to biocomplexity. Complexity is also added by interactions among levels, both upwards and downwards, producing feedback circuits.

Level	Interactions
Ecological communities	Competition, predator-prey, etc.
Populations – species	Reproduction, migration, mortality
Multi-cellular organisms	Environmental interactions, behaviour
Tissues, organs and organ systems	Cell-interactions and organ function
Cells	Specialist behaviour and reproduction
Sub-cellular structures	The 'machinery' of the cell
Molecular networks	Biochemical engines and 'factories'
Molecular surfaces	Lock and key – e.g. enzymes
DNA sequences: codons to genes	Coding and expression control

Please cite this article in press as: Farnsworth, K.D., et al., Functional complexity: The source of value in biodiversity. Ecol. Complex. (2012), doi:10.1016/j.ecocom.2012.02.001

assembly is not only a cardinal attribute of biological systems, it has important consequences for their integrity and resilience (Kolasa, 2005). As a result, even a complete description of genetic information fails to account for the full complement of semiotic information, which is why, for example, seed-banks are no substitute for community conservation, as noted intuitively by Lee (2004) (see also Cowling et al., 2004).

Accordingly, we now define biodiversity as a measure of the total complexity of a biological system (biocomplexity), including complexity at each of the nine levels shown in Table 1. This is equivalent to the total effective information of the system, a substantial amount of which may be found in the genome of its constituent organisms. Crozier (1997) concluded that phylogenetics should form the basis of biodiversity measures, understanding that the goal of biodiversity conservation was to preserve information, much of which is held in the genome. According to Table 1, we must add to this the supra-organism level complexity. Having identified biocomplexity as effective information, we now need to show how it may be quantified, which we do by returning to Bateson's (1972) definition of effect as 'making a difference'. This is formalised by functional information.

3. Functional information

3.1. Up to the species level

In an application of Boltzmann's entropy concept at the genetic level, Szostak (2003) defined 'functional information', in terms of a gene string, as $-\log_2$ of the probability that a random sequence will encode a molecule 'with greater than any given degree of function' – in other words a design brief.

In the case of genes, this 'function' may be thought of as the biochemical activity (for example a digestive enzyme's cleaving rate) of whatever molecule is produced from reading the nucleotide sequence. For a practical degree of function at the DNA level, the probability of a random sequence producing greater function than the observed sequence is approximately zero. This implies that if the information content of the genome were compressed (removing repetition) we would be left with only the functional information content (FIC), but the compressed genome is by definition the algorithmic information content (AIC), hence for the genome FIC = AIC. We acknowledge that there remains considerable debate about redundancy of whole genes within an organism, though many have taken the precautionary approach of assuming all are potentially functional until proven otherwise.

For more than ten years, genetic information has been recognised as an important part of biodiversity (see Crozier's review, 1997). A few economists have adopted this idea to aggregate the genetic information content of an assembly of species through totaling the inter-species genetic-distance (Weitzman, 1992). This was elaborated into the 'Noah's Ark Problem' (Weitzman, 1998), in which a hypothetical choice is made of which species to 'save' in order to maximise the genetic information of the 'Ark'. The problem is expressed in economic terms as finding the optimal level of 'biodiversity', given a budget constraint (or, as recently restated by Béné and Doyen (2008), find 'how big Noah's Ark must be to host the optimal level of biodiversity'). Genetic differences are aggregated into a dissimilarity index and it is assumed that the greater the dissimilarity, the more desirable (hence, valuable) the biological system to which they belong, though Brock and Xepapadeas (2003) make the reasonable complaint that this assumption has not been justified. This is a problem for economists, since, unless information is to be valued in and of itself, it is not clear how maximising genetic diversity maximises welfare. In an alternative approach, Nehring and Puppe (2002) describe species in terms of attribute sets, but their economic valuation entails a subjective choice of attributes which were selected for specific human welfare goals, rather than describing the species' ecological role.

Significantly, these environmental economists have closely linked the idea of unique genetic information to that of function, taking it as axiomatic that genetic information may be valuable only because it codes for potentially valuable functions. These functions are normally thought of as those performed, not by genes, but by whole organisms. The conventional understanding of genetic information in biology is that it provides the 'blue-print' for making the molecular components that are responsible for the complexity and functionality of all the levels between DNA and the whole organism, inclusively. For this reason, the lower seven levels of Table 1 are counted together in considering the functional uniqueness of organisms as a result of genetic-level complexity. Phylogenetic diversity may therefore be used to characterise the information content at and below species level and this contributes to the instrumental value of biodiversity in so far as it constitutes the necessary information for the functioning of those species present in a community (see Lyashevska and Farnsworth, 2012). However, the functionality of most organisms is not directly useful to human society (though there are obvious exceptions): its value is more likely to be the indirect effect of the organism's contribution to ecosystem-level functions: this is the 'contributory value' of 'intermediate goods' (Crocker and Tschirhart, 1992), to which we now turn.

3.2. Beyond the species level

At ecological levels (population and community), Szostak's (2003) functional information approach requires a quantitative specification of the function of each system component (species), from which to find the proportion of 'all possible components' which can fulfil the design brief; but what is the set of all possible components? To the extent that a biological system is composed of a set of inter-dependent components, each optimised by natural selection (for its natural environment), it is composed of approximately unique solutions (Maynard-Smith, 2000). The alternative is that the biological 'design brief' h is specified sufficiently broadly that more than one available design may suffice. If that were true then the FIC of any observed design would, by definition, be less than or equal to its AIC; in all but the special optimal case: FIC $<$ AIC. Accordingly, designs (e.g. species) are substitutable, since there would be more than one way to achieve the design brief. Thus we can think of the ratio AIC/FIC as a measure of substitutability. Clearly, if we specify h and do so in broad terms, such as – 'this ecosystem must sequestrate k tonnes of carbon per year', then there is opportunity for substitutability because FIC is likely to be less than AIC for any particular candidate ecosystem. In that case, we might say that ecosystems are 'over-specified'. However, our choice of h is inevitably arbitrary, partial and subjective. We are, in general, ignorant of the biological design criteria, only able to partially infer them in cases where the loss of system components (e.g. populations) has led to wider measurable ecological effects. In this sense we are in the position of the first brain surgeons, learning which structures do what from studying trauma victims.

3.3. Valuation based on FIC

The ecologically most important development of the economic Noah's Ark idea recognises for the first time that the assembly of 'saved' organisms must work together as a functioning system, not just a 'zoo' (Perry, 2010). To this end, Perry's Noah selects for functional diversity, explicitly recognising 'ecological function' as the contribution to value. However, Perry (2010) defined function

Please cite this article in press as: Farnsworth, K.D., et al., Functional complexity: The source of value in biodiversity. Ecol. Complex. (2012), doi:10.1016/j.ecocom.2012.02.001

only qualitatively and the analysis is limited to a single function, in practice leaving valuation as a subjective choice – of function – by the human valuer. He clearly identified the 'functional uniqueness' of a population as the source of indirect use-value. For Perry (2010), substitutability defines 'ecological importance', by counting the number of populations that perform an identified function in a community (the functional set **F**). His 'ecological importance' measures 'function' in terms of the number of populations affected (members of the affected set **A**). In practice, the network-nature of ecological communities ensures that through indirect effects, **A** contains all of populations in the community. This accords with the established model of an ecological community as a system of differential equations of the form $\partial \mathbf{n}/\partial t = f(\mathbf{n})$, where **n** is the vector of *all* populations. Perry's (2010) measure further assumes that members of a functional group are quantitatively equivalent because the measure is qualitative – a population either contributes to the function or it does not. For this reason, functional populations appear substitutable, though quantitative empirical evidence contradicts that (e.g. O'Gorman and Emmerson, 2009, and references therein).

Despite these caveats, the basic idea, of functional outcome relative to the number of available ways to achieve the outcome, may be used to define 'importance' for community structure as a whole, by applying Szostak's (2003) procedure for calculating FIC. To see this, let **N** be a set of N distinct biological populations (an assembly) and let C_N be an ecological community consisting of the members of **N** and producing some quantified function $R(C_N)$. Further, let $\mathbf{C}_k$ be the set of communities composed of $k \leq N$ populations drawn from **N** and define **C** as the set of communities $\{\mathbf{C}_N, \mathbf{C}_{N-1}, \mathbf{C}_{N-2} \ldots \mathbf{C}_1\}$, forming all the k-combinations of the N elements of C_N for $k = 1 \ldots N-1$ (note $\mathbf{C}_N$ and $\mathbf{C}_1$ both contain a single community). For example, with $k = N-2$, C_{N-2} is the $\binom{N}{N-2}$-member set of communities (using the binomial coefficient) with a pair of populations missing, that is, all the $(N-2)$-member subsets of **N**. Thus **C** is the set of all possible communities which are no more complex than C_N (using only the populations found within it). For any one of these communities C_X, a functional outcome $R(C_X)$ can be quantified, enabling FIC to be calculated as $-\log_2[\Pr\{R(C_X) > R(C_N)\}]$. The probability is given by counting the number of hypothetical communities producing greater function than the observed one (which is also the most complex) and dividing by the sum over k of $\binom{N}{N-k}$, which is the total number of hypothetical communities. In general the set of functional outcomes can only be calculated by modelling each of the hypothetical communities in **C**: an obviously daunting task for the ecological modeller. This is necessary for quantitative functions, since generally the functional contribution from an individual population depends on its ecological context, which is defined by the populations present in the community. However, using Perry's (2010) assumptions for 'ecological importance', we can reduce the calculation to finding the proportion of all possible communities ($C_X \in \mathbf{C}$), having no less than the observed (C_N) function/complexity ratio, where complexity is measured by the number of populations. When affected sets are sub-sets of the whole community, ecological importance is defined as the ratio of affected to functional set size and the calculation involves multiple applications of combinatoric arithmetic. But if we take the scientific view of an ecological community as a dense network of interactions, then Perry's (2010) qualitative importance measure reduces to counting the number of hypothetical communities that achieve the observed level of function $R(C_N)$ (since the affected set of populations is now equal to the community size). Under these assumptions, the highest FIC/AIC ratio is found in the hypothetical community with only one population performing the identified function and the relationship between FIC/AIC and substitutability is transparent.

Whilst it is possible to calculate a FIC/AIC ratio for any ecological community, subject to the strong assumptions discussed, the value found relates to only one of a set of potential functions and should be referred to as the component of FIC contributed by that function. Total FIC is the aggregate of these across all functions and it is that which we should compare with AIC to gauge substitutability. Unfortunately there is no way to specify the complete set of functions, but since functions are likely to differ in their importance, we may consider ranking them and creating a finite set of known functions which reach a threshold of importance. In economics, we may make the ranking an explicit choice, so that we may specify an economically meaningful FIC/AIC ratio and hence quantify substitutability of ecosystem components in relation to an economic choice (a bundle of ecosystem functions).

Functions can be classified into three categories: ecosystem services (functions directly generating social welfare); ecological supports (which create the ecological capacity to provide ecosystem services) and functions with no human consequence, either direct or indirect. Prioritising among these requires some understanding of ecosystem processes to identify the supports which are necessary to maintain important ecosystem services. To simplify, consider a single high priority ecosystem service S. Logically, the sufficient set of supports (**Z**) which are necessary for S is of higher priority than S, since S is impossible without them. Again, it is at least very difficult to identify **Z**, so we are practically forced to rank and select the most important sub-set $\check{\mathbf{Z}}$, based on our best knowledge. But each member, $\check{\mathbf{Z}}_i$, of this subset, itself depends on a set of functions **z**, which must be identified and ordered to form $\check{\mathbf{z}}$ and so on. This procedure continues endlessly, because the dense network inherent in ecological communities is equivalent to a set of loops of functional dependence. If the functional enfolding of the calculation is allowed to be endless, then the mathematical outcome is that all functions will be equally important, even though we are just selecting the most important in each set (since every function will eventually be found to depend on itself). To avoid this uninformative result, we must truncate the implied recursion by assuming that some functions are exogenous to the system (usually meaning abiotic). The obvious place for this truncation is the set of autotrophs – community members with the special property of not needing to consume other organisms in order to live; that is, functional dependencies can most usefully be assumed to end with primary producers.

3.4. Ecological networks of functions

The analysis is simplified by recognising that chains of functional dependency leading from the autotrophs to humanity are an approximate reflection of the food-web structure of the ecological community. By exactly matching the food-web, we make the rather strong assumption that predator-prey and food-competition interactions are the only important functional relationships (but known 'special' relationships, such as pollination or parasitism could be added). This is the assumption behind many community models in practical ecology, especially for marine systems (e.g. Christensen and Pauly, 1992) and amounts to limiting the set of functions to those which transfer energy and matter up through the community, crucially neglecting recycling functions (what we gain from such a gross simplification is the removal of that infinite recursion found in the previous paragraph). If we are prepared to accept the simplification, then a food-web can be used as a web of biological utility-interactions, in which utility is measured by biological fitness – the natural unit of strictly instrumental value for biological systems. Every pair of

Please cite this article in press as: Farnsworth, K.D., et al., Functional complexity: The source of value in biodiversity. Ecol. Complex. (2012), doi:10.1016/j.ecocom.2012.02.001

populations (x, y) in the web is joined by a 'utility valuation' denoting the expected change in biological fitness of x by the presence of y. This is useful because we can now compute aggregate instrumental utility from the 'base-layer' of autotrophic populations to the apex (human society). Representing an interaction between x and y, $V(x, y)$, as a link in a value chain, with a multitude of chains constituting the web (a routed graph, in mathematical terms), then the aggregate over the community can be calculated as $\sum_{\text{chains}}[\prod_{\text{links}}(V(x,y))]$ (note – the product through a chain represents trophic transfer of value (the accumulation of biomass), e.g.: $V(D, A) = V(D, C) \times V(C, B) \times V(B, A)$). In practice, the fitness-value $V(x, y)$ is the expected change in 'reproductive value' of y, due to growth and survival, accrued from y eating x and this is quantified by several ecological models (e.g. Rossberg et al., 2008). The resulting 'value web' model is consistent with and may be compared with the economic theories of the 'contributory value' of 'intermediate goods' (Crocker and Tschirhart, 1992) and the cascading effects of interdependence among species (Norton, 1986).

The food-web analogy, just described, enables us to calculate the value of biodiversity via ecosystem services related to productivity – total biomass, respiration and production rate. These measures, representing the carbon economy of the ecosystem, have established importance in natural resource economics for fisheries and forestry. Using hypothetical (model) foodwebs we can calculate the effect of structural complexity on their function, showing how they are influenced by the distributions of number and lengths of trophic links; number of links per population and the strengths of these links (in short the network properties). These properties are the subject of the assessment of community-level models (e.g. Dunne et al., 2002; Rossberg et al., 2005) which provide a theoretical basis for ecological management, especially of fisheries resources. Including the flows of nutrients such as nitrogen and phosphorus in ecological network analysis (Ulanowicz, 1980) extends to further ecosystem services and the effect of recycling loops in real ecosystems (Ulanowicz and Baird, 1999). Even models which do not explicitly quantify flows have proved useful in identifying the effect of biodiversity on ecological attributes, for example, systems of linked Lotka–Volterra equations show how ecological resistance to climate change, positively correlates with complexity (determined by species number) (Borrvall and Ebenman, 2008).

3.5. A practical example using simulated fish communities

We illustrate the approach using a dynamic food-web model that builds a realistic community by simulated evolution (Rossberg et al., 2008), from which ecological complexity can be quantified. A statistical population of n dynamically stable model communities, $\mathbf{C} = \{C_1, C_2, \ldots, C_n\}$ was generated using parameters that simulate assemblies from the Northeast Atlantic fish community (the model is described in detail by Shephard et al. (2012)). Each community, C_i started with S_i fish species, dynamically coexisting as a foodweb. For each community, individual species were sequentially deleted from the foodweb, which, following this trauma, was allowed to relax to a new equilibrium, this sometimes causing unplanned 'secondary' extinctions. Hence, at each step, $j : S_i \to S_i - (1 + q_{i,j})$, where $q_{i,j}$ counts secondary extinctions. Whenever dynamic equilibrium was reached for a (reduced) model foodweb ($C_{i,j}$), a set of ecological functions was quantified ($\mathbf{R}(C_{i,j})$). $\mathbf{R}$ included biomass measures (e.g. spawning stock biomass, or total mass of large fish) and inter-trophic energy flow-rates, indicating community productivity, as well as the number of secondary extinctions: a surrogate for community stability. Thus $\mathbf{R}$ measures the community against the 'design brief' of a sustainable production of marine biomass. Fish species were chosen for deletion randomly and the sequence of successive simplifications of the foodweb was repeated to generate a population of results from which to calculate mean profiles of $\mathbf{R}(C_{i,j})$. Fig. 1 represents an example community as the population size for each species plotted with its maturation body size and Fig. 2 shows how the mean total fish biomass was affected by simplifications of the community through removal of species (noting that after each species deletion, every remaining population was free to increase in compensation for the loss of species). On average, the first few species deletions affect biomass very little indicating possible redundancy, but after losing 14 species, the community is no longer able to maintain its original level of function. Thereafter, the slope of decline in biomass directly estimates the marginal value of complexity (species richness here) for this ecosystem function. In practice, the various

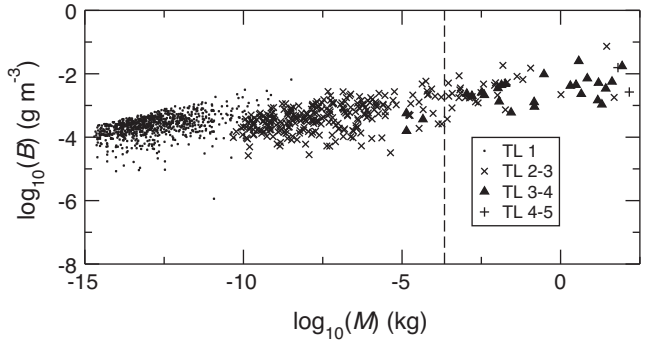

Fig. 1. A simulated ecological community of 1178 species with trophic level coded in symbols, population abundance on the vertical axis and maturation body-size of species on the horizontal axis. All species are fish to the right of the vertical dashed line. The community was built up from zero by successive species invasions. Following each invasion event, population dynamics was run for 200 simulated years, sufficient time to reach equilibrium (typically the case) or near-equilibrium. A total of 33,203 species invasions produced this example community: enough to establish stochastic stability in the number of producers, consumers and total number of species. Shephard et al. (2012) provides details of the model used to produce this community.

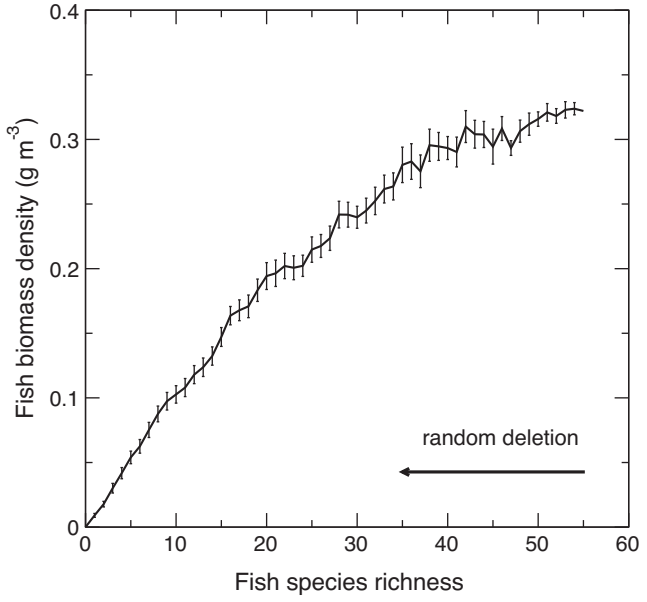

Fig. 2. An ecosystem function (fish biomass produced) varies with community complexity, measured here by the remaining species richness as fish species are sequentially deleted from the model community shown in Fig. 1. Random selection of species identity for deletion gave 30 replicates for every species-richness, from which error bars were calculated. Population-dynamic equilibrium of each reduced-complexity community was ensured before biomass was recorded.

Please cite this article in press as: Farnsworth, K.D., et al., Functional complexity: The source of value in biodiversity. Ecol. Complex. (2012), doi:10.1016/j.ecocom.2012.02.001

elements of **R** can be combined as a weighted-sum, with the weightings subject to an economic decision, or set for a specific ecological goal.

Simulation of the kind just described are supported by experimental manipulations of ecological communities, which have demonstrated the potential for complexity to strongly affect ecological function. For example O'Gorman and Emmerson (2009) selectively removed populations from experimental food webs containing more than 100 species, revealing substantial loss in community diversity, deterioration of stability and reduction of ecosystem process rates, irrespective of the interaction-strengths of the selected populations. Such empirical experimentation is essential, but the networks of ecological functions and their relationship with biocomplexity are so complicated and multivariable that we must augment experimental approaches with modelling. The contribution to services, of any observed complexity, can be estimated with an exploration of hypothetical networks having systematically reduced complexity, as described in the preceding section. The resulting relationship between complexity and service provision can be taken as a benefit function for objective economic valuation: it estimates the marginal value of complexity in units of ecosystem service.

4. Implications

By identifying pattern as 'meaningful' information, distinct from random information, biocomplexity can be resolved within total biodiversity. Following Bateson's (1972) definition of information, we equate this biocomplexity with functional information, which appears in genetic codes (as originally conceived by Szostak (2003)) and also the complexity of ecological networks. This concept of biocomplexity is distinct from the phenomenological property of complexity for which many measures have been described (reviewed by Parrott (2010)). Those measures are insensitive to functional significance and amount to integrative measures of total information content, from which it is impossible to disentangle ecological function. Biodiversity can now be seen as biologically instantiated information, both random and effective, the latter alone being taken to cause biological functions which are the ultimate source of the instrumental value of biological systems.

Present understanding does not give us secure grounds for dismissing any genetic information as random, so total genetic difference still measures the foundation of sub-species value. Phylogenetic methods are already available to do this, though they inevitably require a knowledge of the genome, or at very least the taxonomic position of all the species in the system. Whilst gene-based information is necessary, it is not sufficient for biodiversity to generate instrumental value through function. A collection of living genes could be found in a zoo, or botanical garden or a seed-bank, but these are unable to perform the vital ecosystem services upon which our lives depend (a point well made in the economic context by Norton and Ulanowicz (1992)). Whole functioning ecosystems are needed, the biodiversity of which very much includes the complexity of ecological relationships among participating organisms. This is why complexity at both phylogenetic and ecosystem levels are necessary for an empirical measure of biodiversity (Lyashevska and Farnsworth, 2012). Our adaption of Szostak's (2003) idea to the ecological level provides a method for assessing such complexity in terms of its redundancy, or equivalently, its degree of substitutability, which is the metric needed for economic valuation. However, it is important to recognise that the most economically efficient system is not ecologically optimal, since as Ulanowicz et al. (2009) quantitatively demonstrated, network redundancy provides reserve capacity that is vital in providing systemic resilience.

If biodiversity is the measure of functional information stored in a living system, then we can regard ecosystems as the vaults of information capital. This capital is the organisational basis of autopoiesis for all life (Maturana and Varela, 1980). As such, it may be treated as one of the natural capitals, which sustainability requires us not to deplete (Heal, 1998). Mäler et al. (2009) showed how the ecological accountancy methods, developed and described in Dasgupta and Mäler (2000), can quantify the value of any natural capital (including information), within the context of sustainable development. This gives us a new perspective on biodiversity, seeing it as a depletable natural resource which can be valued in and of itself through the technique of accounting prices (Dasgupta and Mäler, 2000). With this perspective, the value of 'biodiversity' will not be reduced to the value of component species, nor a restricted set of ecosystem services, but rather, it will be an estimate of the information capital estimated by the biodiversity metrics. If these ideas are taken up, the attention will shift towards measuring the complexity of whole systems, in order to value their biodiversity. That will be a significant movement towards ecological realism; more consistent with our scientific understanding of how ecosystems work to provide ecological services.

Acknowledgements

Farnsworth and Lyashevska were supported by a Science Technology Research and Innovation for the Environment grant from the Environmental Protection Agency of the Republic of Ireland: 2007-PhD-SD-3. Farnsworth and Fung were supported by a Beaufort Marine Research Award carried out under the Sea Change Strategy and the Strategy for Science Technology and Innovation (2006–2013), with the support of the Marine Institute, funded under the Marine Research Sub-Programme of the Irish National Development Plan 2007–2013.

References

Adami, C., Ofria, C., Collier, T.C., 2000. Evolution of biological complexity. Proc. Natl. Acad. Sci. U. S. A. 97 (9), 4463–4468.
Bates, M., 2005. Information and knowledge: an evolutionary framework for information science. Inform. Res. 10 (4).
Bateson, G., 1972. Form, substance, and difference. In: Bateson, G. (Ed.), Steps to an Ecology of Mind. University of Chicago Press, pp. 448–466.
Béné, C., Doyen, L., 2008. Contribution values of biodiversity to ecosystem performances: a viability perspective. Ecol. Econ. 68 (1–2), 14–23.
Borrvall, C., Ebenman, B., 2008. Biodiversity and persistence of ecological communities in variable environments. Ecol. Complex. 5 (2), 99–105.
Brock, W.A., Xepapadeas, A., 2003. Valuing biodiversity from an economic perspective: a unified economic, ecological, and genetic approach. Am. Econ. Rev. 93 (5), 1597–1614.
Chaitin, G., 1990.In: Information, Randomness and Incompleteness – Papers on Algorithmic Information Theory, Volume 8 of Series in Computer Science. 2nd edition. World Scientific, Singapore.
Christensen, V., Pauly, D., 1992. ECOPATH-II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61 (3–4), 169–185.
Cowling, R., Knight, A., Faith, D., Ferrier, S., Lombard, A., Driver, A., Rouget, M., Maze, K., Desmet, P., 2004. Nature conservation requires more than a passion for species. Conserv. Biol. 18 (6), 1674–1676.
Crocker, T., Tschirhart, J., 1992. Ecosystems, externalities and economies. Environ. Resour. Econ. 2, 551–567.
Crozier, R., 1997. Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. Annu. Rev. Ecol. Syst. 28, 243–268.
Dasgupta, P., Mäler, K., 2000. Net national product, wealth, and social well-being. Environ. Dev. Econ. 5, 69–93.
de Groot, R., Alkemade, R., Braat, L., Hein, L., Willemen, L., 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. Ecol. Complex. 7 (3), 260–272.
Dunne, J., Williams, R., Martinez, N., 2002. Food-web structure and network theory: the role of connectance and size. Proc. Natl. Acad. Sci. U. S. A. 99 (20), 12917–12922.
Floridi, L., 2003. Information. In: Floridi, L. (Ed.), The Blackwell Guide to the Philosophy of Computing and Information. Blackwell Publishing Ltd, pp. 40–61.

Please cite this article in press as: Farnsworth, K.D., et al., Functional complexity: The source of value in biodiversity. Ecol. Complex. (2012), doi:10.1016/j.ecocom.2012.02.001

Floridi, L., 2005. Is semantic information meaningful data? Philos. Phenomen. Res. 70 (2), 351–370.
Gell-Mann, M., Lloyd, S., 1996. Information measures, effective complexity, and total information. Complexity 2 (1), 44–52.
Gell-Mann, M., Lloyd, S., 2003. Effective complexity. In: Gell-Mann, M., Tsallis, C. (Eds.), Nonextensive Entropy – Interdisciplinary Applications.. Oxford University Press.
Heal, G., 1998. Valuing the Future: Economic Theory and Sustainability. New York, Columbia University Press.
Kolasa, J., 2005. Complexity, system integration, and susceptibility to change: biodiversity connection. Ecol. Complex. 2 (4), 431–442.
Lee, K., 2004. There is biodiversity and biodiversity. In: Oksanen, M., Pietarinen, J. (Eds.), Philosophy and Biodiversity. Cambridge University Press, Cambridge, UK, pp. 152–171.
Lyashevska, O., Farnsworth, K.D., 2012. How many dimensions of biodiversity do we need? Ecol. Indic. 18, 485–492.
MacKay, D.M., 1969. Information, Mechanism and Meaning. MIT Press, Cambridge, MA, USA.
Magurran, A.E., Dornelas, M., 2010. Biological diversity in a changing world. Phil. Trans. R. Soc. B 365 (1558), 3593–3597.
Mäler, K.-G., Aniyar, S., Jansson, R., 2009. Accounting for ecosystems. Environ. Resour. Econ. 42 (1), 39–51.
Margalef, D., 1958. Information theory in ecology. Gen. Syst. Yearbook 3, 36–71.
Maturana, H., Varela, F.J., 1980. Autopoiesis and Cognition: The Realization of the Living. D. Reidel Publishing Company, Dordrecht, NL. Translation of original: De Maquinas y seres vivos. Universitaria Santiago.
Maynard-Smith, J., 2000. The concept of information in biology. Philos. Sci. 67 (2), 177–194.
McAllister, J., 2003. Effective complexity as a measure of information content. Philos. Sci. 70 (2), 302–307.
Mooers, A., 2007. Conservation biology – the diversity of biodiversity. Nature 445 (7129), 717–718.
Nehring, K., Puppe, C., 2002. A theory of diversity. Econometrica 70 (3), 1155–1198.
Norton, B., 1986. On the inherent danger of undervaluing species. In: Norton, B. (Ed.), The Preservation of Species: The Value of Biological Diversity.. Princeton University Press.
Norton, B., 1994. On what we should save: the role of culture in determining conservation targets. In: Forey, P., Humphries, C., Vane-Wright, R. (Eds.), Systematics and Conservation Evaluation. Clarendon Press, Oxford University Press for the Systematics Association, pp. 23–40.
Norton, B., Ulanowicz, R., 1992. Scale and biodiversity policy – a hierarchical approach. Ambio 21 (3), 244–249.
Nunes, P., van den Bergh, J.C., 2001. Economic valuation of biodiversity: sense or nonsense? Ecol. Econ. 39 (2), 203–222.
O'Gorman, E.J., Emmerson, M.C., 2009. Perturbations to trophic interactions and the stability of complex food webs. Proc. Natl. Acad. Sci. U. S. A. 106 (32), 13393–13398.
Parrott, L., 2010. Measuring ecological complexity. Ecol. Indic. 10 (6), 1069–1076.
Perry, N., 2010. The ecological importance of species and the Noah's Ark problem. Ecol. Econ. 69 (3), 478–485.
Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. Nature 405 (6783), 212–219.
Ricotta, C., 2005. Through the jungle of biological diversity. Acta Biotheor. 53 (1), 29–38.
Rossberg, A.G., Matsuda, H., Amemiya, T., Itoh, K., 2005. An explanatory model for food-web structure and evolution. Ecol. Complex. 2, 312–321.
Rossberg, A.G., Ishii, R., Amemiya, T., Itoh, K., 2008. The top-down mechanism for body-mass-abundance scaling. Ecology 89 (2), 567–580.
Sarkar, S., 2002. Defining 'biodiversity': assessing biodiversity. Monist 85 (1), 131–155.
Schrödinger, E., 1944. What is Life? The Physical Aspects of the Living Cell. http://home.att.net/~p.caimi/schrodinger.html.
Shannon, C., 1948. A mathematical theory of communication. Bell Syst. Technol. J. 27 (3 and 4), 379–423 623–656.
Shephard, S., Fung, T., Houle, J.E., Farnsworth, K.D., Reid, D.G., Rossberg, A.G., 2012. Size-selective fishing drives species composition in the Celtic Sea. ICES J. Mar. Sci. 69, 223–234.
Spangenberg, J.H., Settele, J., 2010. Precisely incorrect? monetising the value of ecosystem services. Ecol. Complex. 7 (3), 327–337.
Szostak, J.W., 2003. Functional information: molecular messages. Nature 423 (6941), 689.
Ulanowicz, R., 1980. An hypothesis on the development of natural communities. J. Theor. Biol. 85, 223–245.
Ulanowicz, R., Baird, D., 1999. Nutrient controls on ecosystem dynamics: the chesapeake mesohaline community. J. Mar. Syst. 19, 159–172.
Ulanowicz, R., Goerner, S., Lietaer, B., Gomez, R., 2009. Quantifying sustainability: resilience, efficiency and the return of information theory. Ecol. Complex. 6 (1), 27–36.
Weitzman, M.L., 1992. On diversity. Q. J. Econ. 107 (2), 363–405.
Weitzman, M.L., 1998. The Noah's Ark problem. Econometrica 66 (6), 1279–1298.

Please cite this article in press as: Farnsworth, K.D., et al., Functional complexity: The source of value in biodiversity. Ecol. Complex. (2012), doi:10.1016/j.ecocom.2012.02.001