

1 **Unifying concepts of biological function from molecules to ecosystems.**

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22 **Abstract**

23 The concept of function arises at all levels of biological study and is often loosely and  
24 variously defined, especially within ecology. This has led to ambiguity, obscuring the  
25 common structure that unites levels of biological organisation, from molecules to ecosystems.  
26 Here we build on already successful ideas from molecular biology and complexity theory to  
27 create a precise definition of biological function which spans scales of biological organisation  
28 and can be quantified in the unifying currency of biomass, enabling comparisons of  
29 functional effectiveness (irrespective of the specific function) across the field of ecology. We  
30 give precise definitions of ecological and ecosystem function that bring clarity and precision  
31 to studies of biodiversity-ecosystem function relationships and questions of ecological  
32 redundancy. To illustrate the new concepts and their unifying power, we construct a simple  
33 community-level model with nutrient cycling and animal-plant mutualism, emphasising the  
34 importance of its network structure in determining overall functioning. This type of network  
35 structure is that of an autocatalytic set of functional relationships, which also appears at  
36 biochemical, cellular and organism levels of organisation, creating a nested hierarchy. This  
37 enables a common and unifying concept of function to apply from molecular interaction  
38 networks up to the global ecosystem.  
39

40 **Function as a unifying concept for all levels of biological organisation.**

41

42 Are all the elements of a genome functional or are some junk? Are some species ecologically  
43 redundant or do they all have a unique role? Must a thing be naturally selected before it can  
44 be accepted as functional, or is it sufficient that it causes an effect? These questions all hinge  
45 on the definition we use for function. This became one of the key topics in a recent multi-  
46 disciplinary workshop “Functional Information: its potential for quantifying biodiversity and  
47 its relation to ecosystem functioning”, organised by the Synthesis Centre of Biodiversity  
48 Sciences, Germany. The word ‘function’ has a meaning that may initially seem self-evident  
49 and obvious, but it is used loosely and for many different meanings in biology, creating  
50 ambiguity and uncertainty which matters when we come to quantify e.g. biodiversity  
51 ecosystem function relationships. Here we draw ideas from molecular biology, community  
52 ecology, systems and information theory and philosophy of science to construct a precise and  
53 quantifiable definition of biological function that can unify and focus our thinking on the  
54 questions above. The context in which we write is one of a growing importance for functional  
55 descriptions in ecology (Krause et al., 2014; Stouffer et al., 2012), the rise of metagenomic  
56 functional analysis (Deng et al 2012; Fierer et al., 2012; Howe et al., 2014) and controversy  
57 over functional elements in, especially, the human genome (Kellis et al., 2014; Doolittle et al.,  
58 2014). Because ‘function’ is used differently among sub-disciplines of ecology and wider  
59 biology, our aim here is to promote a unifying meaning, with three goals. First, to enable  
60 cross-fertilisation of ideas through the recognition of a common concept of function, so  
61 making connections and enabling the discovery of more fundamental principles. Second, to  
62 enable communication by using ‘function’ terms in a precisely defined way. Third, to promote  
63 function as a precise, quantitative concept (with units) to establish a common framework for  
64 biodiversity-ecosystem function studies and to enable e.g. objectively based economic  
65 valuation of ecosystem components and diversity (see Farnsworth et al., 2016a). More  
66 deeply, we aim for a definition of ecological function that can illuminate the extent to which  
67 ecosystems are coherent systems, as opposed to mere arbitrary assemblies.

68

69 We start by clearly differentiating between ‘function’ and ‘trait’ in the biological context.  
70 Violle et al., (2007) dispelled much confusion over the term trait, but still today various kinds  
71 of processes and even the values of indices calculated from samples are sometimes  
72 considered ‘traits’ and this is confusing. Here, we restrict function to describe a process (an

73 action) rather than a property of an entity. This leaves the latter to be a trait: a trait is an  
74 inherent property of a biological system (e.g. organism), which may enable a function to be  
75 performed in relation to another system (e.g. a community). For example, the specific  
76 behaviour of hiding certain plant seeds is a trait of some mammals which has the functions of  
77 dispersing the plants as well as providing a continuous food supply for the mammal.  
78 Hypothetically many more functions of this behavioural trait are conceivable, but in practice  
79 we must restrict our considerations to actual (observed) and ecologically relevant functions,  
80 as opposed to potential (hypothesised or not) functions because the full range of potential  
81 functions is indeterminate (e.g. providing food for soil invertebrates may be admissible, but  
82 providing a means of counting the mammals is not, since the latter is not an ecologically  
83 relevant function, but merely a tool of scientific observation).

84  
85 The specific meaning of a function depends on both the functioning entity and the context in  
86 which it acts (function is relational, not inherent). For example a genetic element may code  
87 for a protein only in particular circumstances and a species may promote nitrogen turnover  
88 only in certain environments, therefore they only have those functions in those particular  
89 contexts. The context, in every case, is the system in which the functioning entity takes part.  
90 In a biological setting we refer to this as the next higher ‘ontological level’ recognising that  
91 living systems are composed of a nested hierarchy of organisation: systems constructed from  
92 sub-systems (Farnsworth et al., 2013). An ontological level, in this context, is a structure of  
93 biological organisation that is categorically different from those above and below in the  
94 hierarchy. For example, though a nuclear family and a whole tribe differ in organisational  
95 scale, in category both are units of human society. Conversely a collection of living cells and  
96 a human being are both different in organisational scale and different categories of entity.  
97 More formally, an ontological level (in biology) has associated with it an organisational  
98 structure with the properties of a complex system, especially the property that new  
99 phenomena emerge within it (see also Marshall et al., 2016). An ontological level is always  
100 more than a collection of objects. Thus, for example, a population (defined in the traditional  
101 sense of a mere aggregate, or count, of individuals) is not ontologically distinct from the  
102 individual organism because no properties emerge from the population level, but if the  
103 population is considered as an assembly of genes, then it may qualify as ontologically distinct  
104 from the single genome because emergent properties may appear at the level of gene-  
105 population. Further, a community may be a complex system with an organising structure that

106 leads to emergent properties (e.g. trophic cascades or reaction-diffusion patterns), so we  
107 categorise it as a distinct ontological level. We illustrate how life as a whole can be viewed as  
108 a hierarchy of such ontological levels (Farnsworth et al., 2013) using the ontological  
109 hierarchy given in Table 2, but this does not imply that those *specific* demarkations are fixed  
110 or necessary for our understanding of function.

111

112 From here on, we define biological function with respect to a higher ontological level. We  
113 must carefully distinguish between the terms ecological function and ecosystem function.  
114 Given our axioms, ‘ecological function’ must be an act performed by a living system *within*  
115 *the context of* an ecosystem. That applies equally whether the act is physiological,  
116 behavioural, one of competition, predation or mass-transfer, ecosystem engineering, or  
117 organisational - every branch of ecology can make use of the same concept here. Ecosystem  
118 function is conversely an act performed *by an ecosystem* in some ontologically higher system  
119 - but what? Many ecologists seek a justification for conservation in the ecosystem services (a  
120 result of functions) provided for human society, tacitly assuming humanity to be the wider  
121 context (e.g. deGroot et al., 2012). A non-anthropocentric (objective) account places things  
122 the other way around (indeed this is a central tenet of ecological, as opposed to  
123 environmental, economics (Costanza and Daly, 1987). Objectively, the higher ontological  
124 level of ecosystem function must comprise the global geo-chemical cycle that includes the  
125 biosphere performing certain homeostatic processes (Lovelock and Margulis, 1974).

126

127 In his landmark paper, Jax (2005) resolved the use of the word ‘function’ in ecology into four  
128 broad meanings: 1) individual-level processes, such as a particular predation event; 2)  
129 systemic processes, such as nitrogen uptake; 3) individual ‘roles’ defining ‘functional groups’  
130 of organisms, including their contribution to a higher level of organisation, such as the guild  
131 of detritivores, or simply a phenotypic (often life-history) category and 4) effects of the  
132 activity of working ecosystems that impinge on human society, leading to ecosystem services.  
133 We see immediately that (3) describes a set of functional capabilities of organisms and (1)  
134 describes the realisation of one or more of these in practice, whilst (2) does the same but  
135 takes a coarse-grained view of the system and (4) interprets this from an anthropocentric  
136 perspective.

137

138 In the following, using examples from ecology and molecular biology, we will argue for a

139 more constrained definition of function, in line with (3): that a biological function must  
140 demonstrate **causal effect** (Table 1) from one to a higher ontological level of biological  
141 organisation. This relationship enables us to identify ‘**functional equivalence sets**’ (Table 1),  
142 shifting the focus from particular systems, defined by their traits, to functional classes. This  
143 move enables a logically self-consistent and integrative way to assess all kinds of interaction  
144 in biological systems, by starting from a network of functional equivalence sets. Only by  
145 doing this can we be sure that function has a standard and inter-comparable meaning, in for  
146 example biodiversity-function relationships.

147  
148 **Insights from philosophy and molecular biology**  
149

150 A system composed of parts, each of whose existence depends on that of the whole system is  
151 termed a ‘Kantian whole’ (Table 1), the archetypal example being a bacterial cell (Kauffman  
152 and Clayton 2006). The concept of function arises to describe the role that the parts play in  
153 the system, without having to descend into non-scientific teleology. (Note - the origin of this  
154 terminology lies in Emanuel Kant’s definition of an organised whole (Ginsborg, 2006)).  
155 Accordingly, the philosopher Cummins (1975) proposed that ‘function’ is an objective  
156 account of the contribution made by a system’s component to the ‘capacity’ of the whole  
157 system. Thus *Cummins function* (Table 1) describes a relationship between a system and one  
158 or more of its component parts. The relationship is that at least one process performed by the  
159 component/s is *necessary* for a process performed by the whole system, as in the case of  
160 category (3) of the Jax (2005) schema. This is a powerful idea we shall use from here on.  
161 What we add is clarification about what specifies the ‘whole system’, particularly how it is  
162 bounded, and how this concept can be turned into a tool for quantifying function, especially,  
163 expanding the notion of being ‘necessary’ to a rigorous quantification of causal effect.  
164 Natural selection for a particular component within an organism provides a clear example. In  
165 that case, the component (e.g. an eye) contributes a process that increases the (quantifiable)  
166 Darwinian fitness of the organism, thereby demonstrating Cummins function. The idea, that  
167 ‘true biological functions’ should be naturally selected, has already emerged in the field of  
168 molecular biology, though a broader set of function is advocated by some - as we next  
169 discuss.

170  
171 Recently, thousands of full genomes have been sequenced, not the least being the human

172 genome, and efforts to interpret this new data have stirred up the controversy over ‘junk  
173 DNA’, which is taken to be the alternative to ‘functional DNA’ (see [Kellis et al., 2014](#)). In  
174 this field, little attention has been paid to the precise meaning of ‘function’, despite much  
175 loose talk of ‘functional DNA’. In their criticism, [Doolittle et al., \(2014\)](#) clarified the range of  
176 potential meanings of the term and the conceptual errors that may arise from failing to  
177 resolve them. The most justifiable assignment of function to a DNA element, they argued,  
178 was where selection at the organism level was demonstrated. This is only a subset of cases  
179 where a causal role has been established. Alternatives include a) selection at higher or lower  
180 ontological levels, b) neutral (non-selective) processes, which frequently ratchet their way  
181 into conserved stability, and c) spandrels (the term used by [Gould and Lewontin \(1979\)](#), for  
182 by-products of selection). [Doolittle et al. \(2014\)](#) were careful to distinguish the spandrels from  
183 “mere effects”, which play no causal role in the system to which they belong: spandrels play  
184 an unintended and perhaps irrelevant causal role (e.g. the ‘thumping sound’ of the heart).

185

186 Building on this, we may at least ascribe the word ‘functional’ to biological systems having  
187 causal effects that are known to have been naturally selected for at any level of organisation  
188 subject to natural selection (not only species, but also gene, or genetic network). They are  
189 functional in the Cummins sense and their causal effect can be quantified by the change in  
190 fitness they cause in the system to which they belong. However, this definition would leave  
191 out systems with Cummins function but not derived from natural selection. They would be  
192 left as ‘merely’ causal, rather than biologically functional. These causal systems could be  
193 subsystems of naturally selected systems, for example ‘molecular machines’ (e.g. the ATP  
194 synthase complex), or biochemical networks (examples in [Jaeger and Calkins, 2012](#)), or they  
195 may be super-systems of them: populations or communities of organisms.

196

197 Metagenomic functional analysis challenges this restrictive notion of biological function by  
198 revealing the processes that are being (RNA), or could be (DNA) performed at the  
199 community level of organisation (Tringe et al., 2005; Warnecke et al., 2007; Huttenhower et  
200 al., 2012; Howe et al., 2014). With it, function is readily discerned because the link between  
201 gene expression and functional protein or peptide is usually known and unambiguous,  
202 irrespective of our knowledge of its natural selection. Although eukaryotic organisms  
203 typically present more complicated and often less clear geno-phenotypic links, the method is  
204 also developing for them (see e.g. Knack et al., 2015). These new molecular tools reveal a  
205 literal functioning: the causal chain leading from one biomolecule to the next. The  
206 components (e.g. functional genes) are performing Cummins function for the organism level  
207 (which because of this, performs Cummins function at the community level) and their  
208 performance is well defined and quantifiable. This unambiguous identification of a causal  
209 chain is the ideal towards which ecologists may strive (Gotelli et al., 2012; Bohmann et al.,  
210 2014). Accordingly, we now offer a definition for biological function:

211  
212 **A biological function is a process enacted by a biological system A at ontological level  $n$**   
213 **which influences one or more processes of a system B at level  $n+1$ , of which A is a**  
214 **component part.**

215  
216 This definition is similar to that of Cummins function, but more precisely identifies the link  
217 between ontological levels of organisation. By tracing functional effects through the nested  
218 hierarchy leading from one to the next higher ontological level, it can be made explicit how a  
219 function at the molecular level can be functional at an ecological level. The definition does  
220 not require a history of natural selection and it does not require a 'good' outcome for the  
221 system (as selection would). The latter point answers the philosophical objection often  
222 levelled at scientific accounts of function (see e.g. Griffiths, 1993), which arises from the  
223 teleological (referring to purpose) and normative (what ought to be) connotations of the  
224 every-day use of the word 'function' (a rich literature on philosophical approaches to  
225 biological function is reviewed by Neander (2011)). Our definition creates a clear separation  
226 between these everyday meanings of function and a strict scientific meaning.

227  
228 If functions are strictly processes, then potentially more than one system component can



229 perform them and functional redundancy and substitution become possible. This idea, which  
230 we now incorporate into our definition of function is usefully formalised by the concept of  
231 *functional equivalence class* (FEC) (Table 1), which has grown from analysis of biochemical  
232 networks. The FEC was defined by Auletta et al., (2008) as a set of biochemical ‘operations’  
233 having effects in common which are relevant to ‘goals’. The FEC consists of all operations  
234 (behaviours or processes) having the effect in question and this is context-dependent because  
235 an effect always depends on the nature of both the subject and the object. For example, the  
236 DNA sequences and corresponding protein structures of alcohol dehydrogenases in  
237 vertebrates bear no similarity with those of *Drosophila* and they work through different  
238 chemical reactions, but achieve the same end result of removing hydrogen from alcohol  
239 (Doolittle 1994). Those different dehydrogenating processes form an FEC with respect to  
240 frugivorous organisms (and would not with respect to obligate carnivores). The existence of  
241 alcohols in fruit arises from interactions among plants and micro-organisms (i.e. at the  
242 community level) and exerts natural selection on the metabolic processes (cellular level) of  
243 frugivorous organisms. This illustrates a general feature of FECs: they define the function at  
244 one ontological level in terms of processes at a higher level, which in turn must include at  
245 least one component from among them. Any function specifying an FEC complies with the  
246 definition of Cummins function. Using the FEC generalises the concept by identifying the  
247 source of causation: it is not the individual components performing the function, but the FEC  
248 (i.e. the macro-level unit). This allows for the possibility of functional redundancy and  
249 substitution: both important features illustrated at the ecological level by species turn-over  
250 and at the sub-species level by heterologies and convergence (reviewed by McGhee, 2011).  
251 We next discuss the extent to which this definition of biological function applies in ecology,  
252 with special reference to the biodiversity-function relationship.

253

254

### 255 **At what level do whole ecosystems function?**

256

257 Function in ecological communities had traditionally been thought different from function in  
258 whole or parts of organisms because ecological systems do not fit the conventional model of  
259 Darwinian evolution (Maclaurin and Sterelny, 2008). Recent evidence (e.g. Rillig, et al.,  
260 2015) and an emerging ecological theory of broader evolution (Laland et al., 2015)

261 challenges that view. Niche construction theory (Odling-Smee et al. 1996) and the concept  
262 of reciprocal causation in which organisms influence their evolution via ecological processes  
263 (Laland et al., 2011) both include the ecosystem as an integral part of a complex evolutionary  
264 process.

265

266 The predominance in community ecology of predator-prey networks, described by flows of  
267 energy in foodwebs has emphasised an incomplete model of community structure in which  
268 only one function (energy flow) is admitted, rendering what Loreau (2010) calls ‘horizontal  
269 diversity’ redundant. In every real community, each organism performs more than one  
270 function and functions are more than contributions to energy flow. This has been recognised  
271 in the development of community models based on nutrient-cycling (e.g. Loreau, 1996;  
272 Thébault and Loreau (2003); Loreau (2010) and in the study of mutualistic networks  
273 involving pollinators and seed dispersal (e.g. Schleuning et al., 2015), to which parasites and  
274 ‘ecosystem engineers’ might be added (see e.g. Bruno et al., 2003). As Krause et al., (2014)  
275 explicitly state, ecosystem functioning results from the interactions among organisms, which  
276 though based on organism diversity are a (neglected) form of diversity in themselves. Our  
277 definition of function as strictly relational calls attention to the importance of the interaction  
278 network as a component of diversity and it identifies the organisation (network structure) of  
279 its component ecological functions as the (proximate) cause of ecosystem function. This is a  
280 point we wish to emphasise, especially because so far, the mainstream of studies into  
281 biodiversity / ecosystem function (BEF) relationships has neglected the contribution of the  
282 community network (in and of itself) to ecological functioning (Hooper et al., 2005;  
283 Cardinale et al., 2012), despite contradictory evidence (e.g. Bascompte, 2009; Grey et al.,  
284 2014; Valiente-Banuet et al., 2015). Experimental manipulations that discriminate the effect  
285 of network structure (the organisation of functions at the community level) from organism  
286 effects (the traits enabling ecological functions) will be challenging, but are necessary to  
287 appreciate the extent to which the higher ontological level of community operates.

288

### 289 **What this says about functional redundancy**

290

291 Functional redundancy does not mean that a system will be unaffected by species loss. The  
292 idea that species may be mutually redundant can arise from the neglect of the quantitative  
293 contributions made by *individual* organisms to ecological processes. Functionally

294 substitutability (belonging to the same FEC) does not imply mutual redundancy: an analogy  
295 with members of a tug-of-war team illustrates how individual organisms can be functionally  
296 substitutable, but not redundant. In community ecology, this point is well illustrated by  
297 empirical findings, e.g. from O’Gorman and Emmerson (2009) and Isbell et al., (2011).  
298 Further, we must distinguish between redundancy and degeneracy. Consider a set of  $n$  species  
299  $\underline{S}$ , and a set of  $k$  functions  $\underline{F}$ . We associate a  $k$ -long vector of functions  $\underline{f}_i$  with each member  
300 species  $s_i$ , the values in the vector being the quantified contributions of  $s_i$  to each of the  $k$   
301 functions in  $\underline{F}$ . Now we can transform from  $n$  species to  $m$  functional equivalence sets  $\underline{E}$  by  
302 gathering all those members of  $\underline{S}$  sharing the same  $\underline{f}$ . But being relational, functional  
303 equivalence must be defined relative to the context, i.e. the environmental conditions.  
304 Organisms that are members of FEC  $e_j$  in  $\underline{E}$ , irrespective of environment are qualitatively  
305 redundant, but those that only share  $\underline{f}_j$  in common for a particular environment are merely  
306 degenerate with respect to that environment alone (Tononi et. al., 1999). This is the basis for  
307 the ‘insurance’ justification for biodiversity in the environmental economics literature (Yachi  
308 and Loreau, 1999; Baumgärtner, 2007).

309  
310 Community ecology and especially BEF research has tended to account for one single  
311 species-level Cummins function at a time (e.g. total energy flow), though this constriction  
312 was eased, notably by Gamfeldt et al., (2008) and Isbell et al., (2011) and by attempts to  
313 integrate mutualistic networks along with competition, predator prey and parasitism (see Kefi  
314 et al., 2012 and reviews by Krause et al., 2014 and Namba, 2015). Since each organism can  
315 perform many functions and each function can be performed by many organisms, it makes  
316 sense to transform from networks of species-specific populations to quantitative functional  
317 networks of FECs. Many community ecologists have started to refocus this way (e.g.  
318 Schleuning et al., 2015), aided by increased data from molecular ecology which can more  
319 precisely isolate function (e.g. Zhou et al., 2010; Deng et al., 2012; Fierer et al., 2012). There  
320 is insufficient evidence to claim that any organism is functionally redundant in the  
321 quantitative, multi-functional sense (Gamfeldt et al., 2008, Farnsworth et al., 2012) and we  
322 think it unlikely.

323

324

### 325 **Quantifying function**

326

327 Identifying FECs is a key component of the functional analysis of biological systems.

328 FECs may be equated with observed functions from metagenomic functional analysis (see  
329 e.g. [Fierer et al., 2012](#)) and other identified processes such as metabolism, predation and  
330 specific ecosystem engineering. In practice, this may result in too many classes for  
331 quantitative analysis. We would then be forced (as we usually are) to identify a set of *a-priori*  
332 function classes to which observed functions are assigned. Choosing these classes will  
333 depend on what degree of difference among functions we would consider sufficient to  
334 identify them as separate. This may be objectively estimated from the overlapping of the  
335 functions' effects, for which the concept of 'effective number' in biodiversity ([Jost, 2006](#),  
336 [Chao et al., 2014](#)) was applied to ecosystem processes by [Ulanowicz et al., \(2014\)](#). Observed  
337 functions would be assigned in proportion to both the number of components (enzymes,  
338 populations, etc.) and the effectiveness of the functions in any given environment.  
339 Effectiveness is empirically quantifiable given a precise definition of the function as a  
340 process. For some processes this approach is already well established. For example, predation  
341 is quantified by the individual (per-capita) 'functional response' (see e.g. [Dick et al., \(2014\)](#)  
342 for a relevant application). Ecosystem engineering is often highly context specific, but  
343 empirical approaches have been found (e.g. [Queiros et al., 2011](#)). The approach we are  
344 suggesting calls for a precise definition and identification of FECs, for which the payoff is  
345 likely to be a more robust understanding of how biological systems work.

346

347 As we have defined them, functions are causal. Thus in principle we can quantify them in  
348 both magnitude and direction, according to their causal effect (for which structural equation  
349 modelling and related methods may be useful ([Shiple, 2000](#)). In practice this can be very  
350 difficult for complex systems with reciprocal causation ([Laland et al., 2011](#)), particularly in  
351 the face of limited time-series data samples, latent variables, and incomplete knowledge of  
352 the system under consideration ( see [Sugihara et al., 2012](#) and [Deyle et al., 2016](#)). Recent  
353 developments in information-theoretic and network analysis (e.g. [Zenil et al., 2016](#))  
354 combined with knock-out experiments to discern causal interactions ([Pearl, 2000](#)) provide a  
355 way forward. Measures of functional effectiveness can, in principle, be assessed at and across  
356 different levels of organisation of a system ([Marshall et al., 2016](#)), but application of these  
357 rigorous theoretical measures to ecological systems demands the acquisition of extensive  
358 time-series data.

359

360

361

362 As a specific example consider the (highly simplified) illustrative model community in Figure  
363 1 (detailed description in Appendix), which depicts four trophic levels and five functions:  
364 nitrogen supply (recycling, fixation, nitrification etc.), carbon supply, with the consequent  
365 functions of carbon and nitrogen flow, and reproductive facilitation (e.g. pollination). Note  
366 that the functions are individually quantified in their own *native* units (i.e. units of carbon  
367 flow rate, nitrogen flow rate and e.g. pollination rate). Every function performed in the system  
368 is contingent on every other, because each depends on the biomass and thereby the growth  
369 rate of the species in each FEC providing it. This in turn depends on the species supplying  
370 functions necessary for this growth. Analysis of functional dependencies (Figure 2) shows  
371 that every function ultimately depends on the aggregate community-level biomass production  
372 rate (B), but this in turn depends on every function. This illustrates two important principles:  
373 first that the FECs form an autocatalytic set (*sensu* [Kauffman, 1986](#)) and second that due to  
374 the recursive structure (everything depends on everything else) the system is in [causal closure](#)  
375 ([Table 1](#)) and thereby ([Kauffman and Clayton, 2006](#)) constitutes a Kantian whole. The  
376 closure referred to here is strictly causal and not material, nor thermodynamic. Causal closure  
377 means that the network of causal interactions is sufficient to describe the behaviour at the  
378 system level, given the necessary material and energy supply from the environment ([Hordijk](#)  
379 [& Steel, 2004](#)), acknowledging that living systems are always materially and  
380 thermodynamically open. This causal closure is a general property of the physiology of  
381 individual organisms ([Luisi 2003](#)), many biochemical sub-systems of life ([Kauffman 1986](#))  
382 and as our example illustrates, at least some ecological systems (for which it has important  
383 implications). As an illustration of the mutual dependencies, Figure 3 shows the equilibrium  
384 biomass (excluding nutrient providers) of the community which varies with a) the asymptote  
385 of nutrient providers' functional response and b) the effectiveness of reproduction facilitation  
386 for plants by animals. The community dynamics are tremendously complicated (Appendix) as  
387 is typical of a system with several autocatalytic loops and the result of exogenous  
388 perturbations is determined by internal relationships and correspondingly difficult to predict.  
389

## 390 **The concept of Master Function**

391 Most broadly, a community that can be viewed as a Kantian whole is consistent with a  
392 general definition of life: “A system can be said to be living if it is able to transform external  
393 matter and energy into an internal process of self-maintenance and production of its own  
394 components” (Luisi, 2003, p52). By this definition, all biological function ultimately amounts  
395 to production of living cells and this is readily quantified by biomass. Accordingly, we can  
396 regard biomass production as a ‘master function’ (Jaeger and Calkins, 2012), meaning that all  
397 functions may be quantified by their contribution to it (by analogy, all processes in a factory  
398 may ultimately be quantified by their contribution to the profit made by the factory owning  
399 business). Alternatives to biomass have been inspired by approaches from physics and  
400 computer science: energy dissipation based on thermodynamic theory, e.g. Kaila and Annala  
401 (2008) and diversification based on complexity theory (Kauffman, 2000). We chose to focus  
402 on biomass production because it is most readily measured in practice and also has a clear  
403 biological and evolutionary basis. The idea of a master function removes the need for a  
404 teleological account of function: it is the de-facto end point of the causal chains to which all  
405 other biological functions belong, in the proximal as opposed to ultimate sense of Mayr’s  
406 (1961) dichotomy (modified by Laland et al., 2011). Any biological process which enhances  
407 the fitness of a biological system, increases the system’s potential to reproduce and by this,  
408 over time, it increases the amount of biomass embodying it. Using biomass as the ‘master  
409 function’ means that all functions at all scales of biological organisation can be quantified in  
410 terms of their contribution to biomass production (which may be found *in vivo* by e.g.  
411 species removal, or gene knockouts, or in computational simulations through sensitivity  
412 analysis as illustrated in Figure 3). So whilst every kind of function can be quantified in its  
413 own native units, we can also quantify it in the community context (referring to the function  
414 to which it contributes at the higher ontological level), by its effect on aggregated biomass  
415 production. Notice that this is true at the community level, but also at the level of cells, where  
416 reproduction via completing the cell-cycle is the ‘master-function’ (as illustrated in Jaeger  
417 and Calkins, 2012). In our suggested interpretation, biomass production is a universal  
418 currency for biological function, which integrates ecological function with that defined at any  
419 other level of biological organisation. We can quantify function (of any process) in terms of  
420 the specific change in the rate of creation of cells (fitness), given the presence / absence of the  
421 functional component (this is analogous to the power density proposed by Chaisson (2011) as  
422 a surrogate for complexity). While individual processes of course all appear in different units,

423 the integrative framework proposed enables them all to be interpreted in the common  
424 currency of biomass production, using e.g. mathematical simulations to examine the effect of  
425 removing any functional component upon the production rate of the remaining system,  
426 following recovery to a new equilibrium (as in [Fung et al., 2015](#)).  
427

## 428 **Conclusion**

429 The Biblical lesson of the ‘tower of Babel’ was that division and confusion results from a  
430 fragmentation of language. By establishing a common and precise meaning for the word  
431 ‘function’, we believe a conceptual unity can arise among the various sub-disciplines of  
432 biology. We have found that biological systems at all levels of organisation share the  
433 properties of auto-catalytic sets and that this enables us to summarise the aggregate effect of  
434 ecological functions via specific biomass production rate, which serves as an integrating  
435 surrogate measure of their effectiveness. Specifically, to quantify biological function,  
436 irrespective of whether this is genetic, cellular or ecological (behavioural, physiological,  
437 population, community or process), we suggest the following steps:

- 438 1) Identify the ontological level of the system under study and the next higher ontological  
439 level of which it is a component (Table 2).
- 440 2) Identify the FEC(s) to which the study system belongs (in relation to the higher ontological  
441 level) - this amounts to specifying the system’s functions in terms of relationships among the  
442 parts.
- 443 3) Perform knockout / elimination experiment (or simulation study) to quantify function in  
444 terms of the master function for the higher ontological level (the whole of this level should be  
445 included in the experiment).

446 This approach is now well established in molecular biology for investigating gene regulation  
447 networks, the result of protein expression and signalling networks. It is developing in the  
448 analysis of prokaryotic communities via functional analysis of ‘environmental’ gene sequence  
449 data. Here we have shown that it can be extended to levels of organisation beyond the  
450 individual organism and applied generally in all fields of ecological science, thus integrating  
451 the concept of function and its analysis over all levels of biological organisation.

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Table 1. Glossary of Terms

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**Causal effect:** An effect that can unambiguously be attributed to a process: it only exists when the process is operative.

**Cummins function:** A process performed by a component that is necessary for performance of a higher level process by the system of which it is part.

**Functional Equivalence Class (/Set) (FEC):** The set of components of a system that share in common a particular function in the context of a higher ontological level.

**Kantian whole:** A self-contained system in the sense that the parts make the whole and the whole makes the parts (from raw materials and energy that may be obtained from its environment). In biology, this concept is most useful for characterising auto-catalytic sets in which components collectively by their functions, maintain and create the system to which they belong. The system is interpreted as a higher ontological level than the component parts. The information embodied by the system (at the higher ontological level) which is responsible for the ordering of the interactions among its components at the lower ontological level has been termed a *Transcendent Complex* (Farnsworth et al., 2016b).

**Causal Closure:** In this context (rather than in philosophy in general) closure is defined by Hordijk and Steel (2004) as the condition of an autocatalytic system whereby every reaction is catalysed by at least one component of the system and every reactant is created from a specified ‘food set’ of raw materials, using the reactions of the set. This last condition explicitly acknowledges that the system must be materially open. In general a system may be thermodynamically and materially open, yet causally closed. The Hordijk and Steel (2004) definition gives mathematical rigour to the concept of Kantian whole, i.e. a self-sustaining system supported by a sufficient supply of raw materials and energy: it is causally closed but not thermodynamically nor materially closed.

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495  
496 Table 2.  
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- 
- 499 1) Molecule (including physical structure of informational bio-polymer).
  - 500 2) Molecular network (including information content of bio-polymer, control or signalling
  - 501 system and metabolic pathway).
  - 502 3) Prokaryotic cell and organelle of the eukaryotic cell and a population of such.
  - 503 4) Eukaryotic cell and a population\* of such.
  - 504 5) Multicellular organism and a population\* of such.
  - 505 6) Ecological community, including cellular colony and meta-community.
  - 506 7) The global bio-geo-chemical system of plant Earth.
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508  
509 \* Meta-population is also included, unless inter-population interactions are complex, in  
510 which case, the meta-population would be better categorised as a community.

511  
512 Table 2: An illustrative ontological hierarchy of biological systems. At each level, properties  
513 emerge that cannot be explained by reference to its component parts (existing at the next  
514 lower level) alone. This is because every ontological level is associated with a causal  
515 interaction network among the component parts. The information embodied in this network is  
516 the source of the emergent properties.

517 FIGURE LEGENDS

518

519 Fig 1. An illustrative ecological community consisting of primary producer FECs ( $P_1, P_2$ );  
520 primary consumers ( $C_1, C_2$ ), secondary consumers ( $C_3, C_4$  and  $C_5$ ) and nitrogen suppliers (N).  
521 Thin solid arrows show trophic flows, thin dotted arrows show reproductive facilitation (e.g.  
522 pollination and seed dispersal), thick black dashed arrows show nutrient flow (in isolation)  
523 and grey dashed show waste nitrogen, which is assumed all to return to N. The system can be  
524 envisaged as three parallel functional networks (nutrient recycling, carbon pumping and  
525 reproductive facilitation). Together, these functions catalyse one another so that the whole  
526 system is an autocatalytic-set.

527

528 Fig. 2. Functional dependencies show the community to be an autocatalytic set. In (a)  
529 reproductive facilitation (R) depends on FECs  $C_1$  and  $C_4$ , which in turn depend on biomass  
530 production of  $P_1$  and  $C_2$ , respectively, which in turn depend on nitrogen supply from N and  
531 reproductive facilitation R - forming an autocatalytic loop. The ellipse symbols indicate  
532 'jointly necessary', otherwise parallel inputs are mutually degenerate, or redundant. C: carbon  
533 supply; N: nitrogen supply, B(E) is biomass production rate of the whole community. Note  
534 that all functions ultimately depend on - and result in - B(E). For this reason, B(E) provides a  
535 suitable 'master function' with which to quantify all internal functions.

536

537 Fig. 3. How equilibrium total system biomass B - the master function - varies with the rate of  
538 plant reproductive facilitation by consumer species and also the asymptote of the functional  
539 response of nutrient providers, to supply of raw materials (nutrient FR). The plot was formed  
540 from finite-difference numerical calculations of the system (Appendix equations 6-13). The  
541 dynamics did not converge to an equilibrium for combinations of values, which is the reason  
542 for the few missing and aberrant results (intentionally left visible in the plot).

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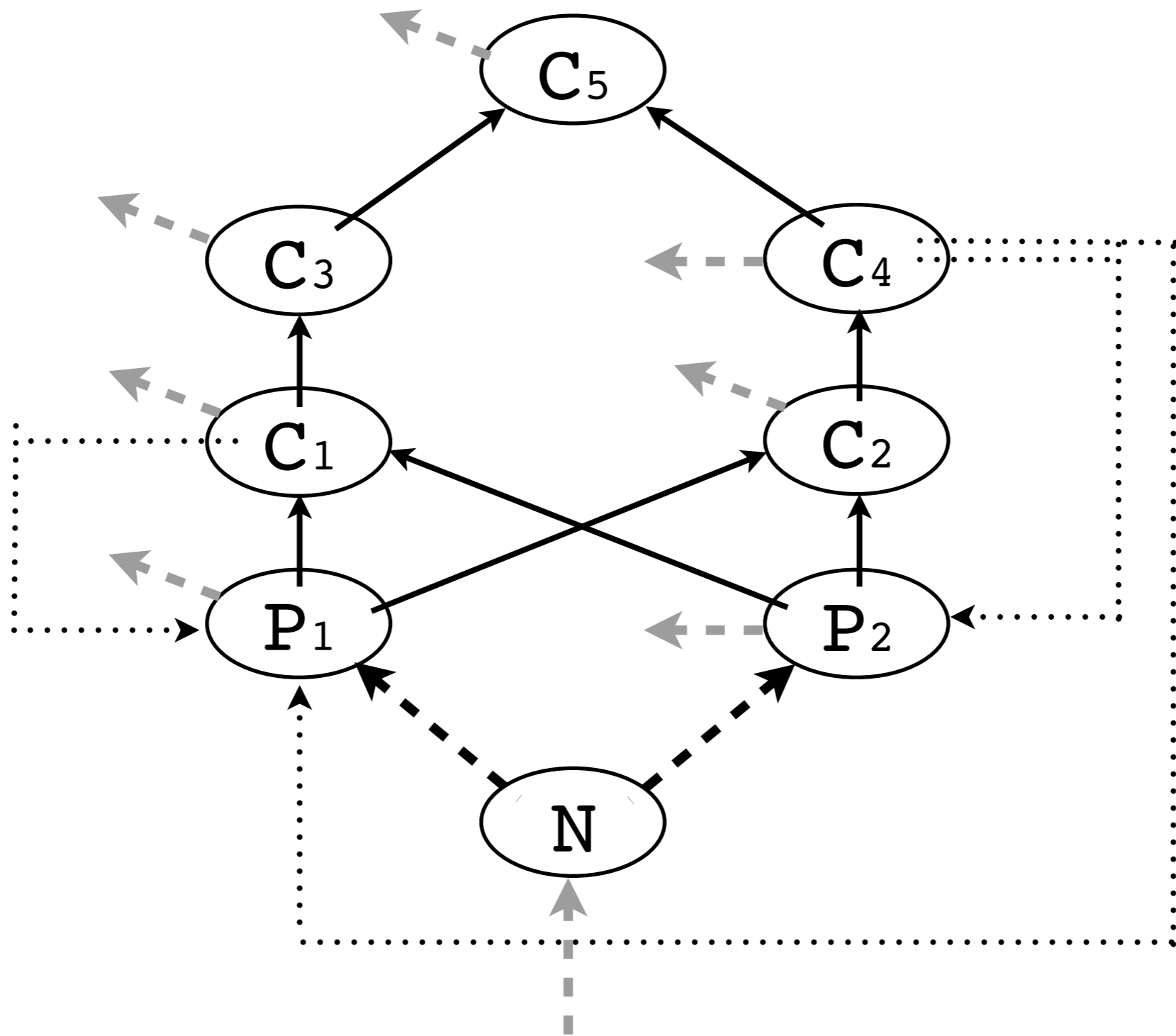
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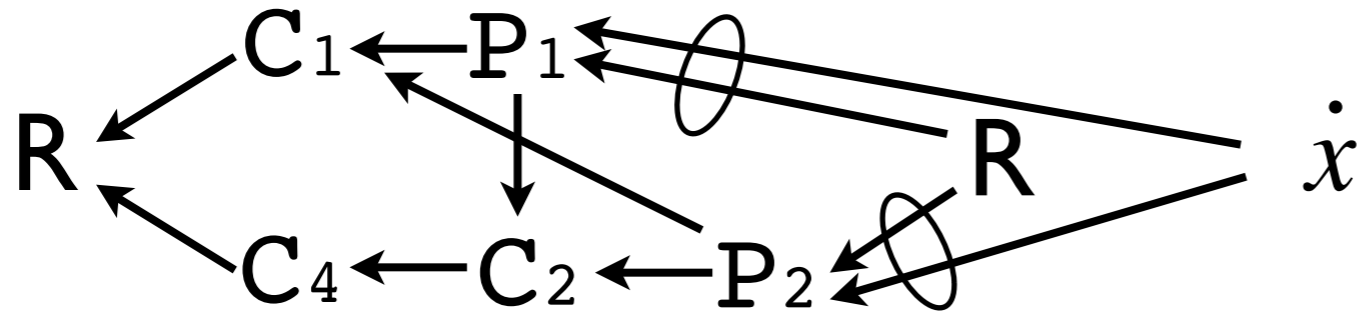
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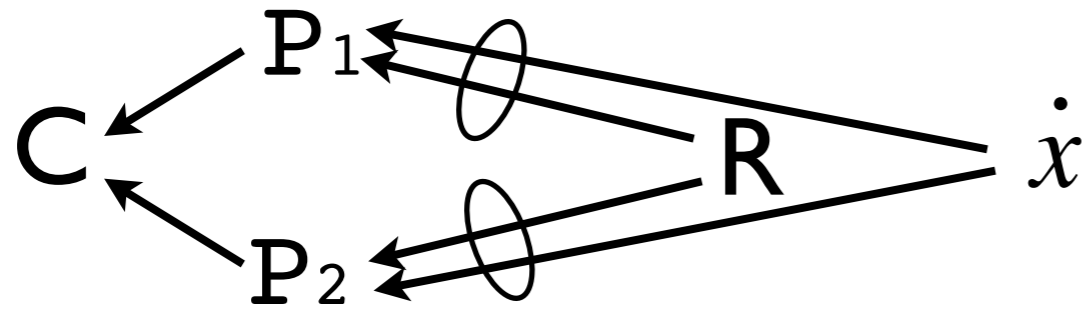
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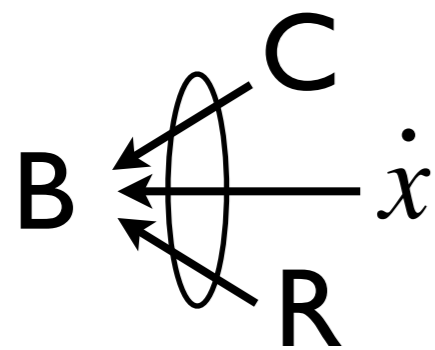




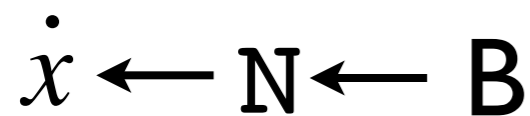
Nutrient flow  $\dot{x}$  catalyses reproduction facilitation R



$\dot{x}$  with R catalyse carbon flow C



$\dot{x}$  with R and C catalyse system biomass B



System biomass catalyses nutrient flow

