

# Equivalence and dissimilarity of ecosystem states

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## Abstract

Measuring (dis)similarity between ecosystem states is a key theme in ecology. Much of community and ecosystem ecology is devoted to searching for patterns in ecosystem similarity from an external observer's viewpoint, using variables such as species abundances, measures of diversity and complexity. However, from the point of view of organisms in the ecosystem, proportional population growth rates are the only relevant aspect of ecosystem state, because natural selection acts on groups of organisms with different proportional population growth rates. We therefore argue that two ecosystem states are equivalent if and only if, for each species they contain, the proportional population growth rate does not differ between the states. Based on this result, we develop species-level and aggregated summary measures of ecosystem state and discuss their ecological meaning. We illustrate our approach using a long-term dataset on the plankton community from the Central European Lake Constance. We show that the first three principal components of proportional population growth rates describe most of the variation in ecosystem state in Lake Constance. We strongly recommend using proportional population growth rates and the derived equivalence classes for comparative ecosystem studies. This opens up new perspectives on important existing topics such as alternative stable ecosystem states, community assembly, and the processes generating regularities in ecosystems.

*Keywords:* Hutchinson niche, ecosystem dynamics, ecosystem dissimilarity, proportional population growth rate, per capita growth rate

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## 1. Introduction

In abstract terms, ecosystem ecology is about identifying deep similarities between superficially different ecosystems. For example, practical problems such as developing ecological indicators (Niemi and McDonald, 2004) rely on having an appropriate concept of the properties of ecosystems which make them similar or dissimilar. Widely-used properties include abundances (Ginzburg, 1983, p. 7), relative abundances (Legendre and Legendre, 2012, p. 328), diversity (Jost, 2006), complexity of energy flow pathways (Ulanowicz, 1986), and aspects of ecosystem functioning such as productivity and material cycling (Loreau, 2010, chapters 3 and 6). However, to an external observer of the ecosystem, there does not appear to be any objective way to determine which of these many properties are relevant,

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9 or how much weight should be given to each. This is of practical importance, because multiple properties of an  
10 ecosystem may change in different ways. Without an objective way to select and weight these properties, different  
11 external observers (for example, government bodies with different priorities) may disagree on whether the integrity  
12 of an ecosystem has improved or deteriorated between two points in time (Andreasen et al., 2001).

13 In contrast, for an organism in an ecosystem, the properties that matter, and how much weight should be given  
14 to each property, are determined entirely by the structure of the Hutchinson niche. An understanding of such  
15 structure is therefore essential to the ideas that follow. In order to see this, we first define proportional population  
16 growth rate to mean the rate of change of abundance per unit of abundance, for example per-capita population  
17 growth rate when abundance is measured in individuals, or mass-specific population growth rate when measured  
18 as biomass. We require that proportional population growth rate is measurement invariant (i.e. does not depend  
19 on the way in which abundance is measured: Cropp and Norbury, 2012). Hutchinson (1957) defined the niche of  
20 an organism as the set of states of the environment permitting a species to persist indefinitely. Later work makes  
21 it clear that by “persist indefinitely”, it was meant that the proportional population growth rate for the species  
22 was non-negative (Hutchinson, 1978, p. 194). Thus, the dependence of proportional population growth rate on  
23 environment is an essential concept in the definition of the Hutchinson niche. The initial view of niche space was  
24 essentially static, with a point in niche space representing the fixed values of (usually non-living) resources in an  
25 ecosystem. Maguire (1973) introduced both structure and dynamics into niche space. Structure was provided by  
26 level sets (contours, if niche space is two-dimensional) of equal proportional population growth rate, and dynamics  
27 by movement of ecosystems through niche space, driven either by external changes or as a consequence of population  
28 growth. Maguire explicitly stated that this view of niche space allows us to examine “the total environment of a  
29 species, a population, or an individual . . . through its ‘biological eyes’”, in other words as an organism within the  
30 ecosystem would see it, rather than as an external observer. Of course, organisms do not “see” population growth  
31 rate, so that the “biological eyes” of a species must be interpreted as the outcome of the process relating population  
32 growth rate to environment.

33 Exponential growth of a population occurs when “nothing happens in the environment” (Ginzburg, 1986). In  
34 other words, exponential growth will occur if and only if the environmental influences on a population do not  
35 change (Turchin, 2003, chapter 2). Note that in general, other populations (and the focal population, in cases of  
36 interference competition) are included in the environment. This law of exponential growth is a basic principle of  
37 population dynamics in a universe without spontaneous generation (Turchin, 2003, p. 24), and can be derived using  
38 a simple Taylor polynomial argument (Hutchinson, 1978, pp. 1-3). However, it is worth thinking about what the  
39 absence of change in environmental influences means, with the aid of three cases:

- 40 (i) it is obvious that if there has been no change in any aspect of the environment, then environmental influences  
41 have not changed, and exponential growth will occur;
- 42 (ii) if an ecosystem moves through niche space from one level set to another (Maguire, 1973; Tilman, 1980, Figure

43 1, solid arrow), environmental influences are changing, proportional population growth rate is changing, and  
44 population growth is not exponential;

45 (iii) if an ecosystem moves through niche space, but remains within a level set (Figure 1, dashed arrow), then  
46 although the environment is changing, environmental influences on the population do not change, proportional  
47 population growth rate does not change, and population growth is exponential.

48 The first and third cases are unlikely to occur in nature, but are important conceptually. In particular, in the third  
49 case, “nothing happens” from the point of view of the organism, even though to an external observer, something  
50 is happening. In general, two ecosystem states which are superficially different can be equivalent from the point  
51 of view of a species if they are in the same level set in niche space and therefore lead to the same proportional  
52 population growth rate. It is necessary to know the structure of the Hutchinson niche in order to distinguish  
53 between the second and third cases. Thus, the most important aspect of this view of the Hutchinson niche is that  
54 the map from environment to proportional population growth rates tells us exactly what properties matter to the  
55 organism, and when two ecosystem states are equivalent.

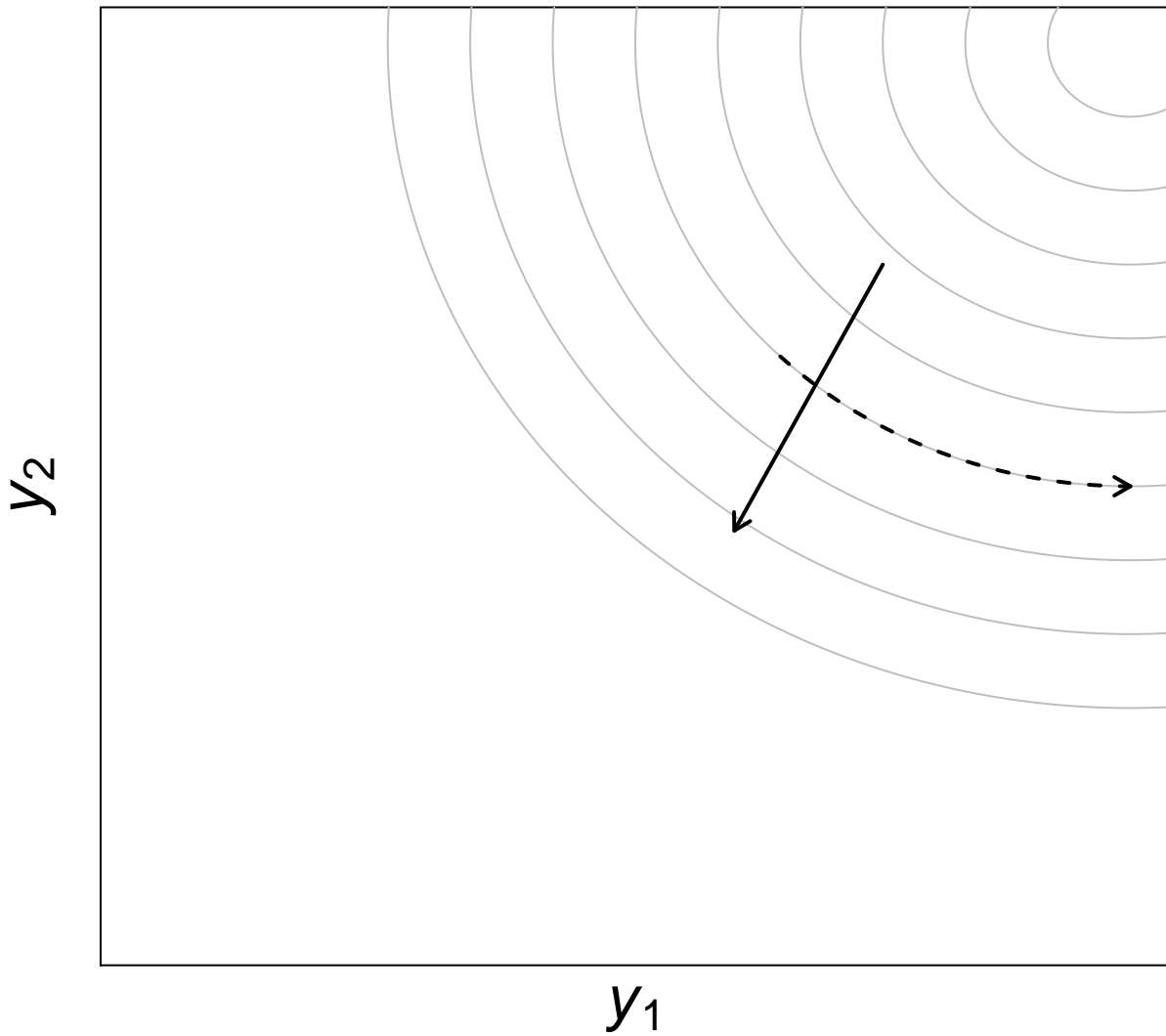


Figure 1: Movement of an ecosystem through a two-dimensional niche space, with axes representing resources  $y_1$ ,  $y_2$ . Any change in position in this space represents a change in the environment. Grey lines: level sets of equal proportional population growth rate for a single species. Solid arrow: movement of the type considered by Maguire (1973) and Tilman (1980), such that the ecosystem state from the point of view of the organism changes. Dashed arrow: movement within a level set, such that the ecosystem state from the point of view of the organism is unchanged.

56 This natural definition of ecosystem state in terms of proportional population growth rates has some important  
57 consequences. For example, two ecosystems which have the same abundance of every species (and may therefore be  
58 viewed as equivalent by an external observer) may or may not be equivalent to the organisms involved. On the other  
59 hand, all internal equilibria of a deterministic system are equivalent. Thus alternative stable states with the same  
60 set of taxa present are invisible in evolutionary terms to the organisms involved. The definition also suggests some  
61 immediate questions. First, applying this definition across all species in an ecosystem leads to a high-dimensional  
62 state. Ecosystem properties visible to an external observer, such as diversity, are often summarized in a low-  
63 dimensional way, for example using diversity indices (Jost, 2006). Can the same be done for the natural measure  
64 of ecosystem state? Second, the relationship between the dynamics of an ecosystem (including all properties that  
65 an external observer could measure) and the dynamics of ecosystem states (as experienced by organisms) may have  
66 important consequences for attempts to explain patterns in ecosystem structure (Borrelli et al., 2015). Natural  
67 selection cannot distinguish between groups of organisms with the same proportional population growth rates. As  
68 a result, there will be variation among ecosystem states (visible to an external observer) on which natural selection  
69 cannot act. To what extent does this limit the role of natural selection as an explanation for ecosystem structure?

70 In this paper, we aim to:

- 71 (i) develop the ideas outlined above about equivalence of ecosystem states from the point of view of the organisms  
72 involved, in a more formal way;
- 73 (ii) clarify the distinction between dynamics on equivalence classes of ecosystems (from the point of view of  
74 organisms) and dynamics as seen by an external observer;
- 75 (iii) identify classes of ecosystems differing in the relationship between these two kinds of dynamics;
- 76 (iv) develop measures of ecosystem dissimilarity and scalar measures of ecosystem state based on proportional  
77 population growth rates.

78 These concepts can be applied either to compare ecosystem states in different locations, or ecosystem states at the  
79 same location at different times. We illustrate the use of summaries of ecosystem state from the point of view of  
80 organisms with data from a plankton system. We discuss the consequences of these ideas for comparative studies  
81 of ecosystems, and the mechanisms that may generate regularities at the ecosystem level.

## 82 **2. Equivalence from the point of view of organisms**

83 **Definition 1.** Let  $\Omega$  be an amount of physical space, i.e. an area or volume in two- or three-dimensional physical  
84 space, respectively. Let  $\mathbf{x} = (x_1, x_2, \dots, x_n)$  be the abundances (e.g. numbers of individuals, if individuals are  
85 well-defined, or cover or biomass otherwise) of all the  $n$  species present in  $\Omega$  ( $x_i \in \mathbb{R}_{>0}, i = 1, \dots, n$ ). Let  $\mathbf{y} =$   
86  $(y_1, y_2, \dots, y_m)$  be the values of all the physicochemical variables affecting any of these species ( $y_i \in \mathbb{R}, i = 1, \dots, m$ ).  
87 Then  $s = \{\Omega, \mathbf{x}, \mathbf{y}\}$  is an *ecosystem state*.

88 Definition 1 is not greatly different from standard usage, but it is necessary to have a precise definition. The  
89 specification of  $\Omega$  as an amount of physical space, irrespective of location, will allow us to make comparisons between  
90 different locations with the same set of species present, as well as between the same location at different times.

91 **Definition 2.** Let  $S$  be the set of ecosystem states  $s \in S$  in which exactly the same set of  $n$  species are present, and  
92 let  $\alpha$  be any function with domain and codomain  $S$ . Then  $S$  is an *ecosystem*, and  $\alpha$  is an endomap of  $S$  (Lawvere  
93 and Schanuel, 2009, p. 15), describing ecosystem dynamics within  $S$ .

94 Again, our definition of ecosystem is close to standard usage. In what follows, we assume for simplicity that  
95 dynamics operate in discrete time. Essentially the same arguments as those below can be made in continuous time,  
96 the only difference being that there must then be an endomap  $\alpha_t$  for each real number  $t$ , satisfying  $\alpha_0 = 1_S$  (the  
97 identity in  $S$ ) and  $\alpha_{t+u} = \alpha_t \circ \alpha_u$ , i.e. the composition  $\alpha_t$  following  $\alpha_u$  (Lawvere and Schanuel, 2009, p. 169). Note  
98 that the definition above does not require us to say anything about what kind of function  $\alpha$  is. We later develop  
99 ideas about the consequences of different classes of endomaps for ecosystem dynamics (Section 4), and discuss a  
100 particular example (Equation 4), but at this stage, the theory remains general.

101 Let  $r_i : S \rightarrow \mathbb{R}$  be a function from the set  $S$  of ecosystem states to the real numbers  $\mathbb{R}$  such that  $r_i(s)$  is the  
102 contribution of endogenous processes (e.g. births and deaths) to the proportional growth rate of the  $i$ th species.  
103 In general, we assume that this may depend on both abundances  $\mathbf{x}$  and physicochemical variables  $\mathbf{y}$ , although we  
104 later give special cases in which it depends on only one of these. In a finite population,  $r_i(s)$  is interpreted as the  
105 expected value over demographic stochasticity. There is no need to consider environmental stochasticity, because by  
106 definition, all the variables that affect  $r_i$  are specified in the ecosystem state  $s$ . We do not require that the ecosystem  
107 state  $s$  is part of a closed system, but we do not include immigration and emigration in  $r_i(s)$ . This is consistent  
108 with the view that immigration and emigration should not be considered when determining the suitability of an  
109 environment for a species, which resolves some of the problems with connecting the definition of a niche to the  
110 distribution of a species (Drake and Richards, 2017). In what follows, for conciseness we sometimes simply refer to  
111 “proportional population growth rate”: unless otherwise specified, this refers only to the endogenous component of  
112 this growth rate.

113 To the  $i$ th species, two ecosystem states  $s, s' \in S$  are equivalent if and only if  $r_i(s) = r_i(s')$  (i.e. the contributions  
114 of endogenous processes to proportional population growth rate are equal). As argued above, when this condition  
115 is satisfied, the two ecosystem states lie in the same level set in niche space for the  $i$ th species, so that from the  
116 point of view of the species, “nothing happens” if we move from one to the other, even though the ecosystem states  
117 may appear different to an external observer. In other words, a unit of abundance of the  $i$ th species in ecosystem  
118 state  $s$  would neither benefit nor suffer in evolutionary terms if exchanged with a unit of abundance of the same  
119 species from ecosystem state  $s'$ . Let  $\sim_i$  be the relation defined on the set of ecosystem states  $S$  by  $s \sim_i s'$  if and  
120 only if  $r_i(s) = r_i(s')$ . This is an equivalence relation because it is reflexive, symmetric and transitive (Halmos, 1974,  
121 p. 28). The elements of the quotient set  $S/\sim_i$  (the equivalence classes of  $\sim_i$  in  $S$ ) are the level sets in niche space  
122 for species  $i$ , provided that the abundance of any species having a direct effect on  $r_i$  is included as a niche axis

123 (Maguire, 1973).

124 **Definition 3.** Let  $r$  be the function

$$r : S \rightarrow \mathbb{R}^n \\ s \mapsto (r_1(s), \dots, r_n(s)),$$

125 which maps ecosystem states to  $n$ -tuples of real numbers representing contributions of endogenous processes to  
126 proportional population growth rates of all species. Because the set of such  $n$ -tuples is important, it is worth giving  
127 it a symbol ( $R$ ) and a name: the growth space of the ecosystem (Spencer, 2015), with the value of the function  
128  $r(s)$  being a point in growth space. We henceforth call this a growth state to differentiate this term from the (more  
129 generally defined) ecosystem state. Let  $\sim$  be the relation on the set of ecosystem states  $S$  defined by  $r$  (i.e.  $s \sim s'$   
130 means that  $r(s) = r(s')$ ). Again, this is reflexive, transitive and symmetric, so it is an equivalence relation. Then  
131 we say that ecosystem states  $s, s' \in S$  are *equivalent* (from the point of view of every species) if and only if  $s \sim s'$ .  
132 In other words, two ecosystem states are equivalent if and only if for each species, the endogenous component of  
133 proportional population growth rate does not differ between them.

134 The elements of the quotient set  $S/\sim$  are the intersections of the quotient sets  $S/\sim_1, \dots, S/\sim_n$ , i.e.  $S/\sim =$   
135  $S/(\cap_{i=1}^n \sim_i)$ . In biological terms, these are the intersections of a given set of level sets for each species in niche  
136 space. Note that some of these intersections may be empty. Studying intersections of sets in niche space has been  
137 productive in the past. For example, Hutchinson (1957) focused on intersections of the sets  $r_i \geq 0$  (the niche of a  
138 species, where it has non-negative proportional population growth rate), and Tilman (1980) focused on intersections  
139 of the level sets  $r_i = 0$  (the boundary of the niche), in order to study the potential for coexistence. However, the  
140 intersections of other level sets are also biologically important, a point we return to in the discussion.

141 We do not assume that either the endomap  $\alpha$  (Definition 2: the function describing ecosystem dynamics) or  
142 the function  $r$  from ecosystem states to proportional population growth rates of all species (Definition 3) has any  
143 particular form. In general, the equations describing ecosystem dynamics are unknown. For example, the Lotka-  
144 Volterra equations can usefully be thought of as a second-order Taylor polynomial approximation to some more  
145 complicated system (Hutchinson, 1978, p. 117), but there are few situations in which one would believe that these  
146 are the true equations. It is possible to constrain the form of the functions  $r_i$  that describe endogenous contributions  
147 to proportional population growth rate based on a few axioms (Cropp and Norbury, 2015). Although we do not  
148 follow this up here, it may lead to a deeper understanding of the range of possible dynamics on equivalence classes.

149 We also do not assume that specifying the function  $r$  from ecosystem states to proportional population growth  
150 rates is sufficient to specify the ecosystem's endomap  $\alpha$ . Although endogenous dynamics are important, immigration  
151 and emigration of organisms, and external factors influencing environmental conditions, must also be specified in  
152 order to know the future state of an ecosystem. Closed ecosystems have received more theoretical attention, but  
153 ecosystems with input and output of nutrients and organisms can have qualitatively different dynamics (Loreau  
154 and Holt, 2004).

### 155 3. Ecosystems as objects in the category of sets with endomaps

156 A category can be thought of as a set of objects  $A, B, C, \dots$  and a set of arrows  $f, g, h, \dots$ , such that:

- 157 1. Each arrow  $f$  has some object  $A$  as its domain (source) and some object  $B$  as its codomain (target);

- 158 2. There is an identity, consisting of an arrow  $1_A$  for each object  $A$  with domain and codomain  $A$ ;
- 159 3. Any pair of arrows  $f, g$  such that the codomain of  $f$  is the domain of  $g$  can be composed to form a composite
- 160 arrow  $g \circ f$  from the domain of  $f$  to the codomain of  $g$ ;
- 161 4. Composition is associative, i.e.  $h \circ (g \circ f) = (h \circ g) \circ f$ ;
- 162 5. Composition satisfies the unit laws, that for arrows  $f$  with codomain  $B$ , and  $g$  with domain  $B$ ,  $1_B \circ f = f$
- 163 and  $g \circ 1_B = g$ ;

164 (Lawvere and Schanuel, 2009, p. 21).

165 For example, a set of ecosystem states  $S$  with an endomap  $\alpha$  describing ecosystem dynamics is an object in the

166 category of sets with endomaps (Lawvere and Schanuel, 2009, p. 136). An arrow  $f$  in this category from a set  $X$

167 with endomap  $\gamma$  to a set  $Y$  with endomap  $\delta$  must preserve the structure of the endomap, in the sense that it must

168 satisfy

$$f \circ \gamma = \delta \circ f. \quad (1)$$

169 Intuitively, this means that we can either follow dynamics on  $X$  and then map the result to  $Y$ , or map to  $Y$

170 and then follow the corresponding dynamics of the result on  $Y$ . Thus the dynamical structure on  $X$  defined by the

171 endomap  $\gamma$  is preserved in the structure on  $Y$  defined by the endomap  $\delta$ .

#### 172 4. Classes of ecosystem dynamics

173 Dynamics on a set of ecosystem states  $S$  (visible to an external observer) induce dynamics in growth space  $R$  (as

174 experienced by organisms in the ecosystem). We want to know whether these dynamics have the same structure,

175 in the sense of Equation 1. We need to specify an endomap  $\beta$  on  $R$ : the natural choice is described in Appendix

176 A. Next, we construct a function  $\phi : S \rightarrow S$  such that  $s \sim s' \iff \phi(s) = \phi(s')$ . Then we can show (Appendix A)

177 that dynamics on the set of equivalence classes preserves the structure in ecosystem dynamics if and only if

$$\phi(s) = \phi(s') \implies (\phi \circ \alpha)(s) = (\phi \circ \alpha)(s') \quad \text{for all } s, s' \in S. \quad (2)$$

178 This means simply that the endomap  $\alpha$  describing ecosystem dynamics on the set of ecosystem states  $S$  must not

179 separate members of equivalence classes.

180 It is useful to distinguish three classes of ecosystem dynamics, based on whether and how Condition 2 is satisfied:

181 (a) Condition 2 holds because  $\phi \circ \alpha = \phi$ , so  $r$  is a map in the category of sets with endomaps. Some of the possible

182 ways this could occur are:

183 (i) If  $\alpha = 1_S$ , then  $\phi \circ \alpha = \phi$ , and Condition 2 holds. This is the trivial case in which ecosystems never

184 change.



185 (ii) Note that  $\phi$  is idempotent (i.e.  $\phi \circ \phi = \phi$ ), since  $(\phi \circ \phi)(s) = \phi(s^*) = s^* = \phi(s)$ , for any  $s \in S$ . Hence  
186  $\alpha = \phi$  also satisfies Condition 2, and is not equal to  $1_S$ , provided that at least one equivalence class has  
187 more than one member. There is no obvious biological example of this case.

188 (iii) If resource levels change over time, but in such a way that  $r$  (the vector of endogenous contributions to  
189 proportional population growth rates for each species) remains constant (as in Figure 1, dashed arrow),  
190 then  $\alpha \neq 1_S$ , but  $\phi \circ \alpha = \phi$ . This could in principle be achieved in a controlled laboratory system, but  
191 does not appear likely in nature.

192 (iv) Finally and most importantly, consider an infinite well-mixed space  $\Omega$ , and a set of species interacting  
193 only through resource depletion and production of waste products. The proportional growth rate of each  
194 species depends on physicochemical variables  $\mathbf{y}$ , but not on abundances  $\mathbf{x}$  (so that, for example, there is  
195 no interference competition or predation), and will not in general be zero. Thus in a closed system, we  
196 expect abundances  $\mathbf{x}$  to change over time, so  $\alpha \neq 1_S$ . Furthermore, because  $\Omega$  is infinite and well-mixed,  
197  $\mathbf{y}$  does not change over time, so proportional growth rates do not change over time and the abundance of  
198 each species grows or declines exponentially. Thus in this case, ecosystem states change, while remaining  
199 in the same equivalence class, and Condition 2 is satisfied. This Malthusian situation is an important  
200 starting point for theory, analogous to the role of a body with no forces acting on it in physics (Ginzburg,  
201 1986). In the real world, a similar situation can be realized in a chemostat in which the ecosystem is open  
202 and proportional population growth rates are constant but not necessarily zero, while abundances in the  
203 system do not change.

204 (b) Condition 2 holds even though  $\phi \circ \alpha \neq \phi$ . In other words, ecosystem states change equivalence class over time,  
205 but these dynamics keep members of the same equivalence class together, so that the function  $r$  describing en-  
206 dogenous contributions to proportional population growth rates is a map in the category of sets with endomaps.  
207 There are several possible examples.

208 (i) Suppose that the function  $r$  describing endogenous contributions to proportional population growth rates  
209 depends on the ecosystem state  $s$  only as a one-one function of a single physicochemical variable  $y$ , and that  
210 changes in abundances  $\mathbf{x}$  do not affect  $y$ . Then each equivalence class of  $S$  contains ecosystem states with  
211 a single value of  $y$ , but potentially differing in  $\mathbf{x}$ . Changes in  $y$  will lead to dynamics among equivalence  
212 classes, but the members of an equivalence class will stay together. In idealized stream or soil ecosystems,  
213  $y$  could represent detritus, and  $\mathbf{x}$  detritivores with pure donor-controlled dynamics (Pimm, 1982, p. 136),  
214 with change over time caused by variation in input and output of the resource. Alternatively,  $y$  could  
215 be an environmental variable whose effects dominate all other variables, with change over time caused by  
216 extrinsic environmental variability.

217 (ii) Suppose that proportional population growth rates in a closed system depend only on abundances  $\mathbf{x}$

218 through the relative abundances  $\boldsymbol{\rho} = (\sum_{i=1}^n x_i)^{-1} \mathbf{x}$ , and not on physicochemical variables  $\mathbf{y}$ . Then all  
 219 ecosystem states with abundances of the form  $c\boldsymbol{\rho}$ , for fixed  $\boldsymbol{\rho}$ , will be in an equivalence class, and will be  
 220 mapped to the same new equivalence class by the function  $\alpha$  describing ecosystem dynamics (Appendix B).  
 221 Ecosystems of this kind have purely frequency-dependent dynamics, implicitly assumed in models based  
 222 only on relative abundances (the term “frequency dependence”, which is well established in the ecological  
 223 literature, means only that dynamics depend on relative abundances). Arditi and Ginzburg (2012, section  
 224 6.1) argue that this kind of scaling invariance may be a desirable property. Frequency dependence is  
 225 certainly possible (e.g. Hutchinson, 1978, pp. 134-135), and is sometimes likely to be important. For  
 226 example, if space is limiting, and all the available space is always filled, frequency dependence may be the  
 227 dominant way in which abundances affect proportional population growth rates.

228 (c) In most cases, Condition 2 will not be satisfied, and so  $r$  (the endogenous contributions to proportional popu-  
 229 lation growth rate) will not be a map in the category of sets with endomaps. For example, consider a closed  
 230 ecosystem containing a single species of phytoplankton with abundance  $x$ , whose proportional population growth  
 231 rate  $(1/x)(dx/dt)$  depends on the concentrations of nitrogen ( $N$ ) and phosphorus ( $P$ ), which are used during  
 232 growth but not recycled. This is another case in which endogenous contributions to proportional population  
 233 growth rates depend only on physicochemical variables  $\mathbf{y}$ . A simple model for such an ecosystem, from Maguire  
 234 (1973), is

$$\begin{aligned} \frac{dx}{dt} &= x \left( r_{\max} - \sqrt{a(N - N^*)^2 + b(P - P^*)^2} \right), \\ \frac{dN}{dt} &= -c \frac{dx}{dt}, \\ \frac{dP}{dt} &= -d \frac{dx}{dt}, \end{aligned} \tag{3}$$

235 where  $r_{\max}$  is the maximum possible proportional population growth rate, attained at optimum concentrations  
 236  $N^*, P^*$  of nitrogen and phosphorus respectively, parameters  $a$  and  $b$  determine how quickly proportional popu-  
 237 lation growth rate declines as nitrogen and phosphorus concentrations, respectively, are moved away from the  
 238 optimum, and  $c, d$  are quantities of nitrogen and phosphorus needed to produce a unit of biomass, respectively.  
 239 The space  $\Omega$  is not explicitly defined, but  $s = \{\Omega, x, N, P\}$  is an ecosystem state. Consider the endomap  $\alpha$   
 240 describing ecosystem dynamics defined by

$$\begin{aligned} \alpha : S &\rightarrow S, \\ \{\Omega, x_0, N_0, P_0\} &\mapsto \{\Omega, x(1), N(1), P(1)\}, \end{aligned} \tag{4}$$

241 where  $x_0, N_0, P_0$  are initial values, and  $x(1), N(1), P(1)$  are solutions of Equation 3 after one unit of time.  
 242 Applying this map to some of the ecosystem states in the equivalence class  $\{s \in S : r(s) = 1\}$  (Figure 2, bold  
 243 black line) gives sets of ecosystem states (Figure 2, black lines: each line corresponds to a different value of  $x_0$ )  
 244 which cut contours of proportional population growth rate (Figure 2, grey lines) and thus separate equivalence  
 245 classes.

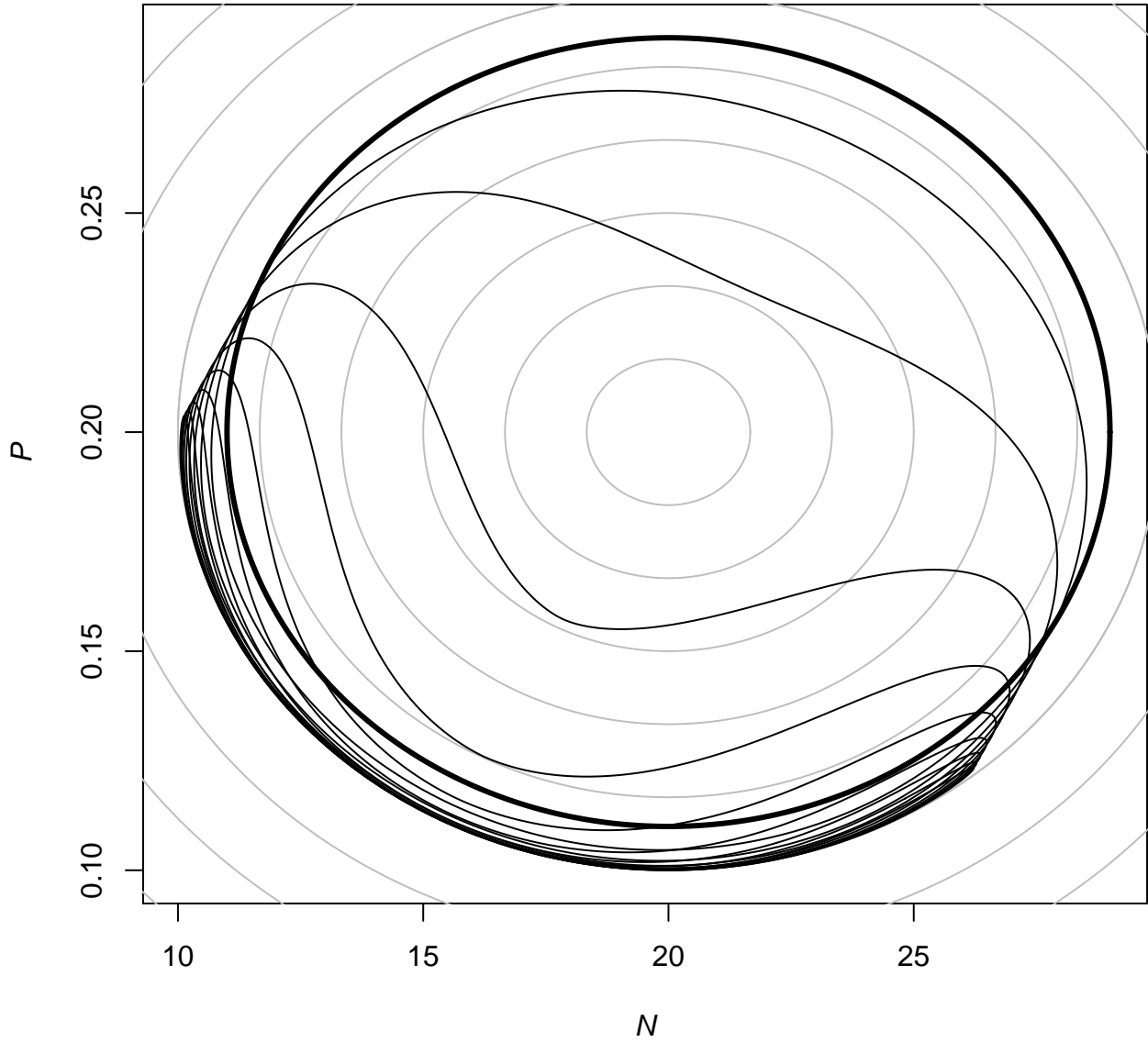


Figure 2: An ecosystem model in which the map  $\alpha$  describing ecosystem dynamics does not preserve equivalence classes. The  $x$ - and  $y$ -axes are concentrations of nitrogen ( $N$ ) and phosphorus ( $P$ ) in arbitrary units, and define a two-dimensional niche space. Grey lines are contours of constant proportional population growth rate  $r$  (level sets in niche space). The bold black line is the contour  $r = 1$ . Thin black lines are some of the values to which the contour  $r = 1$  is mapped after one unit of time by Equation 3 (each line represents a different initial abundance  $x_0$ , between 0 to 5). Solutions obtained numerically. Parameter values:  $r_{\max} = 10$ ,  $N^* = 20$ ,  $P^* = 0.2$ ,  $a = 1$ ,  $b = 1 \times 10^4$ ,  $c = 6$ ,  $d = 0.12$ .

## 246 5. Ecosystem dissimilarity and summaries of growth state

247 It is unlikely that two real ecosystem states will ever be exactly equivalent. In empirical work, it may therefore  
248 be useful to measure how far two ecosystem states are from being equivalent. This is analogous to the common  
249 approach of measuring dissimilarity between ecosystems (Legendre and Legendre, 2012, chapter 7), but from the  
250 point of view of the organisms involved. What properties should be possessed by a measure of how far from  
251 equivalence two ecosystem states  $s_1, s_2$  are? Let  $d(s_1, s_2)$  be such a measure. Convention suggests that we should  
252 have  $d(s_1, s_2) \geq 0$  for all  $s_1, s_2 \in S$ . It will usually be sensible to require that  $d(s_1, s_2) = 0$  if and only if  $r(s_1) = r(s_2)$   
253 (i.e. the two ecosystem states are equivalent). There is in general no reason to privilege one ecosystem state over  
254 another, so it is natural to require that  $d(s_1, s_2) = d(s_2, s_1)$ . A measure with all these properties is a semimetric  
255 (Legendre and Legendre, 2012, p. 295). There are many measures with these properties, of which the most obvious  
256 is Euclidean distance, which also satisfies the triangle inequality, and is therefore a metric (Sutherland, 2009, p.  
257 39): this last property may not be necessary, but is at worst harmless, and is often useful. We will therefore work  
258 with Euclidean distance in what follows. It may be useful to think of this measure as describing dissimilarity in  
259 niche space, as well as in growth space.

260 Given that the growth state  $r(s)$  of an ecosystem (the  $n$ -tuple of proportional population growth rates for all  
261 the species it contains at the time) is typically high-dimensional, it is natural to ask whether and how it can be  
262 summarized. Any function of  $r(s)$  is invariant under dynamics within an equivalence class, and might therefore be  
263 considered as a summary of growth state. In contrast, anything which is not a function of  $r(s)$  will separate measures  
264 of the same equivalence class, and is therefore not a summary of growth state. As a first example of something that  
265 is a valid summary of growth state, proportional population growth rates are likely to be unknown for most species  
266 in an ecosystem. In practice, it will be necessary to work with the  $m$ -tuple of proportional population growth rates  
267 that are known, where  $m < n$ . Since this is a function of  $r(s)$ , it is a summary of growth state. It will often be the  
268 case that proportional population growth rates can be calculated for higher taxa or guilds, but not for individual  
269 species. Strictly speaking, such aggregation is only valid if the species being aggregated have identical proportional  
270 population growth rates at all times. This is unlikely to be exactly true, but may often be approximately true.  
271 Ordination (Legendre and Legendre, 2012, chapter 9) can be done from the point of view of organisms, rather than  
272 that of an external observer, given dissimilarities in growth space. An ordination based on points in growth space,  
273 rather than in abundance space, is a valid summary of growth state because it is a function of  $r(s)$  alone, and may  
274 be a useful low-dimensional approximation of growth state.

275 Scalar summaries are also of interest. Under the view that proportional population growth rates represent the  
276 state of an ecosystem, scalar summaries of growth state will correspond to what are conventionally viewed as scalar  
277 summaries of change. However, many commonly-used measures of “rate of succession” such as Euclidean distances,  
278 Bray-Curtis distances and chi-square distances among relative abundances, reviewed in Spencer (2015, Appendix  
279 B), are not measures of growth state, because they can take more than one value for the same value of  $r(s)$ , and

280 therefore split up equivalence classes. In contrast, the Living Planet Index (Loh et al., 2005) is a scalar summary  
281 of growth state, because it depends only on  $r(s)$ . Two closely-related measures of growth state are size change and  
282 shape change (Spencer, 2015; Yuan et al., 2016). Size change is the mean of the elements of  $r(s)$ , and shows whether  
283 a typical taxon or guild is increasing or decreasing in abundance. Shape change is the sample standard deviation of  
284 the elements of  $r(s)$  and shows the extent to which different taxa or guilds are changing in abundance in different  
285 ways. The rate of competitive exclusion for a pair of taxa or guilds  $i, j$  is defined as  $r_i(s) - r_j(s)$  (Pásztor et al.,  
286 2016, p. 122). It is easy to show that the square of shape change is proportional to the expected squared rate  
287 of competitive exclusion over all pairs of distinct taxa or guilds (Spencer, 2015, Appendix C), and is therefore a  
288 property of a typical pair.

## 289 6. Example: Lake Constance plankton

290 In this section, we summarize the seasonal patterns of growth state for the plankton community in Lake Con-  
291 stance. The theoretical concept of equivalent ecosystem states is applied to a real-world setting using empirical data  
292 on population growth rates from one particular ecosystem, changing its state throughout time. Boit and Gaedke  
293 (2014) describe the typical seasonal cycle of the plankton community in Lake Constance, using splines fitted to  
294 biomass of 20 planktonic guilds over a standardized year, averaged from 1987 to 1996. Plankton samples were taken  
295 weekly during the growing seasons (Apr-Nov) and approximately bi-weekly during the winter months. Rather than  
296 investigating the raw data in each year, we work here with a statistical model to cancel out most of the inter-annual  
297 variability caused by stochastic weather events. Averaging over several years extracts the overarching, general pat-  
298 terns from the empirical data set which then fulfils three requirements: 1.) it contains the same set of species over  
299 time, 2.) it consists of long-term, frequent observations spanning multiple generations, 3.) it reveals the internally  
300 driven dynamics of the food web. The last point is important because in Lake Constance, predator-prey interactions  
301 induce annually repeating changes in population abundances of several orders of magnitudes over a few weeks during  
302 the growing season (Boit and Gaedke 2014). This makes Lake Constance an especially well-suited case study for in-  
303 vestigating growth states largely independent from external (abiotic) forcing data. Proportional population growth  
304 rates  $r_i(s)$  (in  $\text{days}^{-1}$ ) were estimated as differences in spline-interpolated natural log biomass between successive  
305 days (Figure 3). Hence, the spline interpolation represents hypothetical daily observations during a typical year in  
306 Lake Constance. Daily growth rates represent the relevant time-scale for investigating plankton dynamics in Lake  
307 Constance as the fastest eucaryotic organisms (unicellular algae) reproduce daily by division (Sommer, 1985) which  
308 sets the pace of life for their multicellular predators, e.g. daphnids with a generation time of about 1 week.

309 The first three principal components of the proportional population growth rates  $r(s)$  describe 78% of the  
310 variation in the seasonal cycle (Figure 4). The ordination suggests that the ecosystem in May, June and July is  
311 relatively distinct from the rest of the year, when proportional population growth rates are much closer to zero. May  
312 and June are the late spring and clear water phases, when the most extreme positive and negative proportional

313 population growth rates occur (Figure 3, shaded areas) while the ecosystem undergoes a major reorganization  
314 from an early resource-driven to a more mature, resource-limited successional state (Boit and Gaedke, 2014). In  
315 particular, in the late spring phase (May), characterized by algal dominance (Boit and Gaedke, 2014), most of  
316 the algal guilds (Alg2, Alg3, Alg4, Alg5: Figure 3b, c, d, e), autotrophic picoplankton (APP: Figure 3f), and  
317 medium and large ciliates (Cil3, Cil4, Cil5: Figure 3k, l, m) have generally negative proportional population growth  
318 rates, while single-celled algae (Alg1: Figure 3a), rotifers (Asp, Rot1, Rot2, Rot3: Figure 3g, r, s, t), cladocerans  
319 and calanoid copepods (Dap: Figure 3o), and the cladocerans *Leptodora* and *Bythotrephes* (Lep: Figure 3q) have  
320 generally positive proportional population growth rates. In the clear water phase (June), characterized by temporary  
321 dominance of daphnids and a temporary inversion of the biomass pyramid (Boit and Gaedke, 2014), small coccal  
322 algae (Alg5, Figure 3e), autotrophic picoplankton (APP, Figure 3f) and large carnivorous rotifers (Asp, Figure 3g)  
323 have generally negative proportional population growth rates, while most of the algae (Alg2, Alg3, Alg4: Figure  
324 3b, c, d), ciliates (Cil1, Cil2, Cil3, Cil5: Figure 3i, j, k, m) and the cladocerans *Leptodora* and *Bythotrephes* (Lep:  
325 Figure 3q) have generally positive proportional population growth rates.

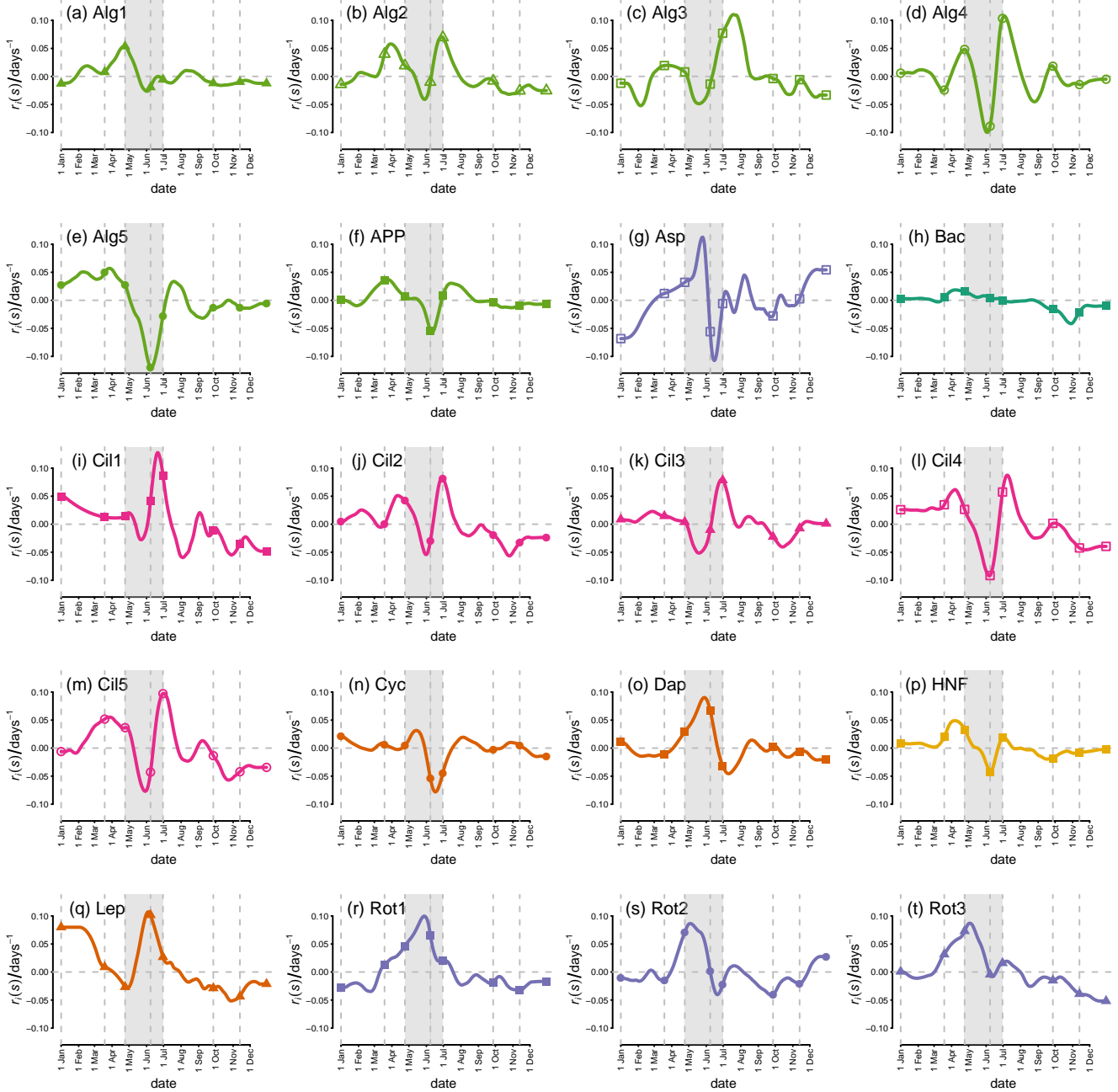


Figure 3: Proportional population growth rates  $r_i(s)$  (in  $\text{days}^{-1}$ ) for 20 planktonic guilds over the seasonal cycle in Lake Constance (data from Boit and Gaedke, 2014). Proportional population growth rates were estimated from splines fitted to biomass over a standardized year, averaged over 1987-1996. Guilds are (a) Alg1 (single-celled algae), (b) Alg2 (mostly large, single-celled algae or colonies), (c) Alg3 (filamentous blue and green algae), (d) Alg4 (diatoms, colonies, filamentous/spiky algae), (e) Alg5 (small, coccal algae), (f) APP (autotrophic picoplankton), (g) Asp (large carnivorous rotifers), (h) Bac (heterotrophic bacteria), (i) Cil1 (small bacterivorous ciliates), (j) Cil2 (small bacterivorous/herbivorous ciliates), (k) Cil3 (medium-sized herbivorous ciliates,  $\log_2(\text{mean body mass / pg carbon}) = 12$ ), (l) Cil4 (medium-sized herbivorous ciliates,  $\log_2(\text{mean body mass / pg carbon}) = 13$ ), (m) Cil5 (larger ciliates), (n) Cyc (cyclopoids), (o) Dap (cladocerans and calanoid copepods), (p) HNF (heterotrophic nanoflagellates), (q) Lep (cladocerans *Leptodora* and *Bythotrephes*), (r) Rot1 (small rotifers), (s) Rot2 (medium-sized rotifers), (t) Rot3 (large omnivorous rotifers). Vertical dashed lines separate phases of plankton succession, from left to right: late winter; early spring; late spring (shaded); clear water (shaded); summer; autumn; early winter. Horizontal dashed lines: zero population growth.

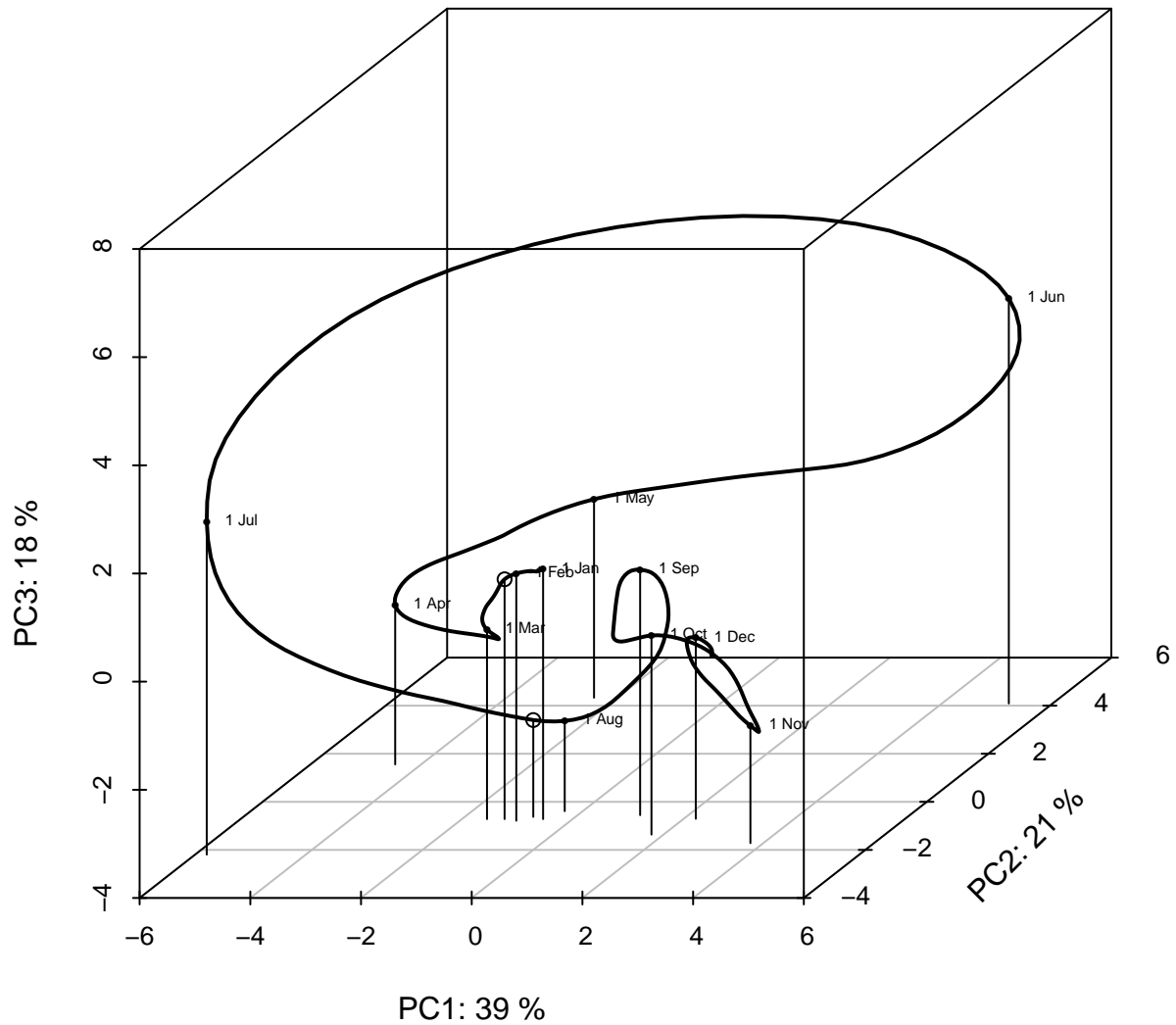


Figure 4: The first three principal components of proportional population growth rates  $r(s)$  for 20 planktonic guilds over the seasonal cycle in Lake Constance (data from Boit and Gaedke, 2014). Together, these three principal components explain 78% of the variation in  $r(s)$ . Proportional population growth rates were estimated from splines fitted to biomass over a standardized year, averaged over 1987-1996. Open circles: days 37 and 210 of the year, on which both size change and shape change were very similar (see Figure 5).



326 In Lake Constance, there are two annual peaks in size change, corresponding roughly to the spring and summer  
327 blooms, separated by a local minimum at the boundary between the late spring and clear water phases (Figure  
328 5(a), white line between shaded regions). This local minimum occurs because at the start of the clear water phase,  
329 most guilds have negative proportional population growth rates (Figure 3), due to dominance of daphnids (Boit  
330 and Gaedke, 2014, Figure 1b). In contrast, shape change is highest in the late spring and clear water phases (Figure  
331 5(b), shaded regions), because although the proportional population growth rates are low for many guilds, they  
332 vary substantially among guilds (Figure 3). Thus, shape change behaves very differently from Lewis's measure of  
333 rate of succession (Lewis, 1978), which has a deep local minimum between the spring and autumn blooms (Boit  
334 and Gaedke, 2014, Figure 4B). Lewis's measure, which is widely used by plankton ecologists, is not a function of  
335  $r(s)$  alone (Spencer, 2015, Appendix B), and therefore is not a measure of growth state in the sense used here.

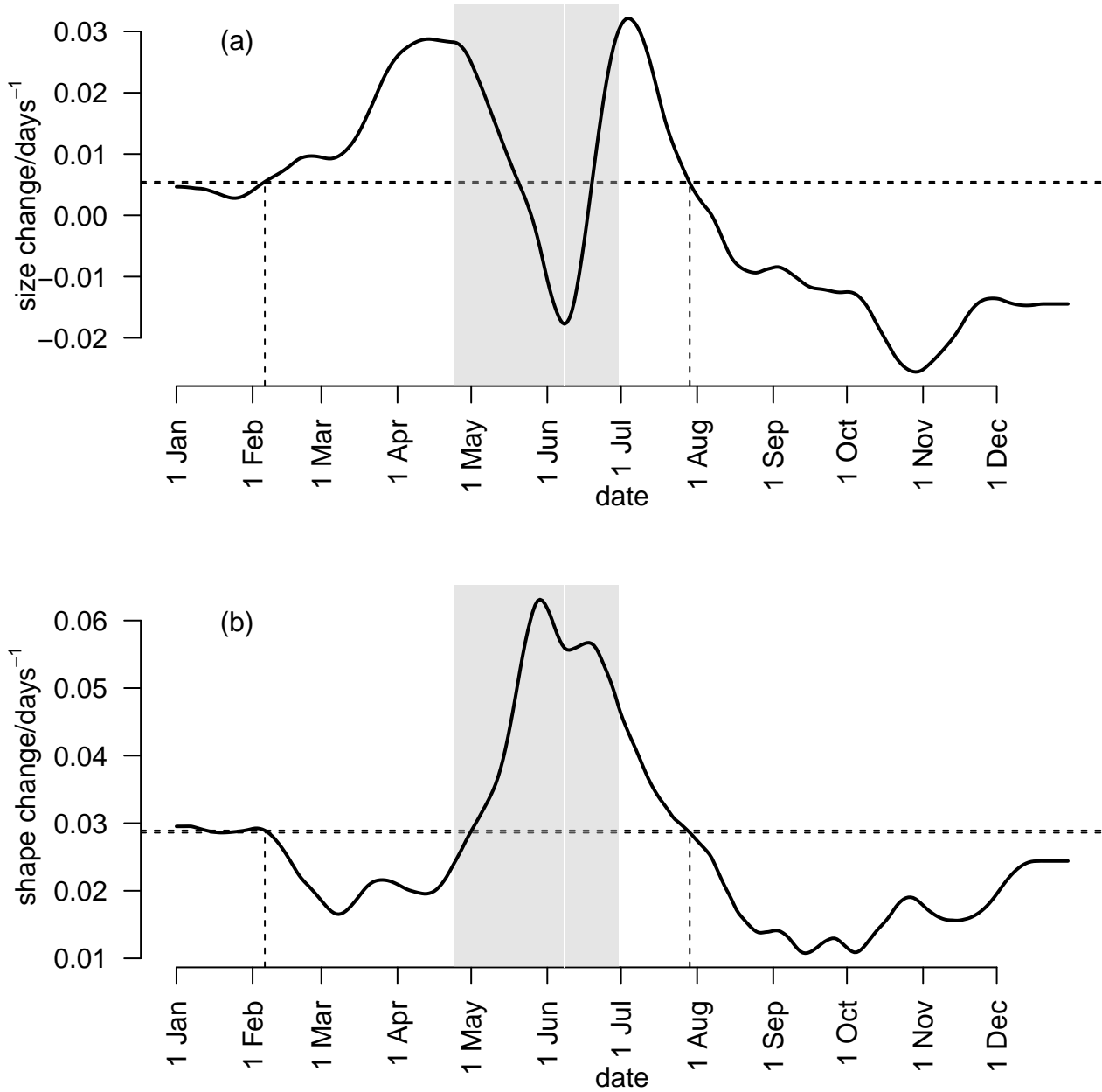


Figure 5: Size change (a) and shape change (b) for 20 planktonic guilds over the seasonal cycle in Lake Constance (data from Boit and Gaedke, 2014). Proportional population growth rates were estimated from splines fitted to biomass over a standardized year, averaged over 1987-1996. Dashed lines: days 37 and 210 of the year, on which both size change and shape change differed by less than  $5 \times 10^{-4} \text{ days}^{-1}$  and the corresponding values of size and shape change. Shaded rectangles: the late spring (left) and clear water (right) phases of the seasonal cycle.

336 Although scalar summaries are appealing in their simplicity, two ecosystems with the same value of one or more  
337 of these functions may not be equivalent from the point of view of any species. For example, both size change and  
338 shape change in Lake Constance differ by less than  $5 \times 10^{-4} \text{ days}^{-1}$  between days 37 and 210 (Figure 5, dashed  
339 lines), and yet the ordination makes it clear that the growth state of the ecosystem is very different on these days  
340 (Figure 4, the open circles are far apart). In fact, 11 out of 20 guilds have proportional population growth rates  
341 with different signs between these days, and the Pearson correlation between proportional population growth rates  
342 on these dates is  $-0.33$ . To understand the differences in more detail, it is necessary to look at the proportional  
343 population growth rates for each guild (Figure 6). The mean and standard deviation are almost identical on both  
344 days (Figure 6, filled black circles and vertical lines), and the ranges are similar (Figure 6, symbols other than filled  
345 black circles). Nevertheless, the identities of the guilds with proportional population growth rates far from zero  
346 differ considerably between the two days, and no guild has exactly the same proportional population growth rate  
347 on both days (Figure 6, none of the coloured lines is horizontal). The guild with the lowest proportional population  
348 growth rate on day 37 is Alg3 (filamentous blue and green algae), which has the highest proportional population  
349 growth rate on day 210. The Lep guild (the cladocerans *Leptodora* and *Bythotrephes*) has the highest proportional  
350 population growth rate on day 37, but a proportional population growth rate slightly below the mean (Figure 6,  
351 right-hand filled circle) on day 210. The Cil1 guild (small ciliates) has the lowest proportional population growth  
352 rate on day 210, but a rate above the mean (Figure 6, left-hand filled circle) on day 37. In summary, even a valid  
353 scalar summary of the growth state of an ecosystem, such as size change or shape change, may not give a good  
354 picture of the state of the ecosystem as experienced by any particular species.

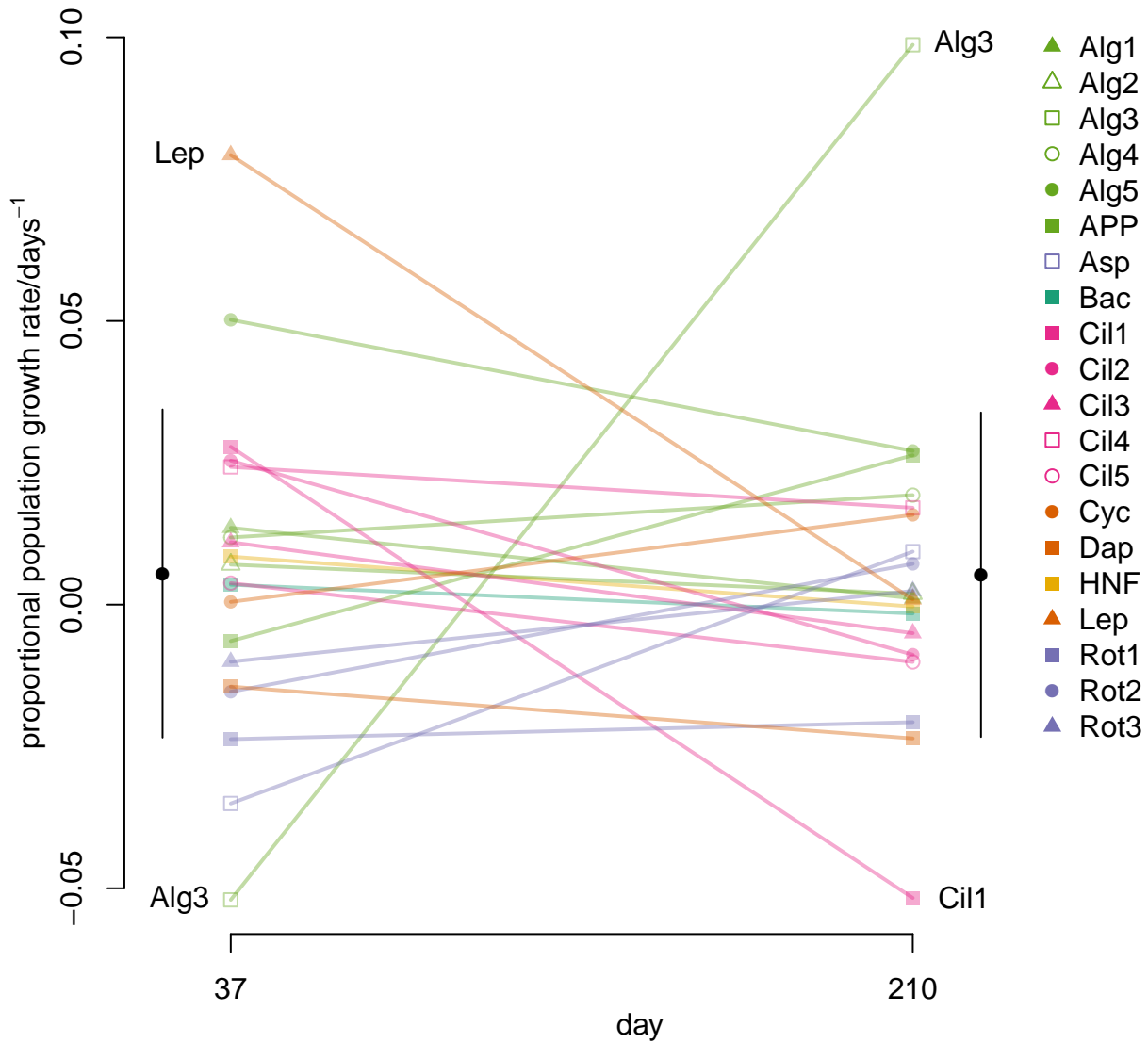


Figure 6: Proportional population growth rates for 20 planktonic guilds in Lake Constance on days 37 and 210 of the seasonal cycle, when both size change and shape change differed by less than  $5 \times 10^{-4} \text{ days}^{-1}$  (data from Boit and Gaedke, 2014). Filled black circles are means for each date, and vertical bars are  $\pm$  one standard deviation. Symbols other than filled black circles are proportional population growth rates for each guild. Lines connect guilds on the two dates. The guilds with the highest and lowest proportional population growth rates on each date are labelled: Lep is the cladocerans *Leptodora* and *Bythotrephes*, Alg3 is filamentous blue and green algae, and Cil1 is small bacterivorous ciliates. Other guild abbreviations as in Figure 3. Proportional population growth rates were estimated from splines fitted to biomass over a standardized year, averaged over 1987-1996.

## 355 7. Discussion

356 We argued above that two ecosystem states are equivalent if and only if for each species, the proportional  
357 population growth rate does not differ between the states. Much of community and ecosystem ecology is devoted  
358 to searching for patterns in variables such as species abundances or relative abundances, measures of diversity and  
359 measures of complexity. However, we showed that except in special circumstances, the dynamics of an ecosystem  
360 as experienced by the organisms in it (in terms of proportional population growth rates) will not be the same as  
361 the dynamics seen by an external observer who focuses on some other property. A consequence of our argument is  
362 that many of the traditional activities of community and ecosystem ecology will not lead to a deeper understanding  
363 of how organisms experience ecosystems. Instead, it may be more productive to search for patterns in proportional  
364 population growth rates. This change in approach comes with new challenges, such as finding appropriate ways to  
365 understand patterns in large numbers of proportional population growth rates. It also opens up new perspectives  
366 on important existing topics such as alternative stable states, the development of ecosystems over time, and the  
367 processes generating regularities in ecosystems.

368 A natural consequence of the arguments developed here is that proportional population growth rates should  
369 occupy a more central position in community and ecosystem ecology, just as they are currently at the heart  
370 of population ecology (Pásztor et al., 2016, p. 5). One challenge is that estimating proportional population  
371 growth rates is more difficult than estimating abundances. In order to estimate proportional population growth  
372 rates, abundance estimates must be obtained at a minimum of two time points. However, this difficulty is not  
373 insurmountable. Furthermore, we propose to do more than just replace snapshots of abundance with monitoring  
374 changes over time. By using proportional population growth rates as measures of ecosystem state, properties other  
375 than abundances (for example, rates of nutrient cycling) are implicitly considered, to the extent that they are  
376 important to organisms, through their effects on proportional population growth rates. Another challenge is that  
377 communities and ecosystems usually contain large numbers of species, and it can be difficult to understand and  
378 summarize the resulting high-dimensional patterns in proportional population growth rates. We showed that an  
379 ordination based on principal components of proportional population growth rates (Figure 4) was able to describe  
380 most of the variation in growth state in Lake Constance. We also showed in Section 5 that it was possible to  
381 construct valid scalar summaries of the growth state of Lake Constance (size change and shape change: Figure 5).  
382 However, two dates with almost identical size change and shape change in fact had very different growth states,  
383 because the identities of the guilds with proportional population growth rates far from zero were different (Figure  
384 6). The dynamics of the two summary indices reveal the pattern of community reorganization during the clear water  
385 phase at one glance, complementing the population-level perspective. Overall, the example from Lake Constance  
386 suggests that more thought is needed about the ecological meaning of summaries of growth state. For example, size  
387 change and shape change tell us about properties of typical taxa or guilds, and of typical pairs of taxa or guilds,  
388 respectively. However, they do not tell us about properties of particular taxa or guilds. The same is true of the

389 closely-related Living Planet Index (Loh et al., 2005), an important statistic in global conservation biology. The  
390 change from particular to aggregate properties demands a justification which is currently lacking, in the same way  
391 that studying biodiversity per se (an aggregate property) rather than the particular species in an ecosystem (each  
392 contributing to the aggregate property) demands a justification (Maier, 2012, pp. 75-76).

393 Our approach can be used to generalize the idea of alternative stable states to that of alternative equivalent  
394 states. Identifying alternative stable states is a challenging problem (Petraitis, 2013). However, if these states  
395 contain the same set of species, they are all equivalent to the organisms involved. Their distinctive feature is  
396 that the equivalence class in which all species have zero proportional population growth rate consists of more than  
397 one disjoint subset. More generally, when proportional population growth rates depend on multiple interacting  
398 resources, each with a finite optimum value (Tilman, 1980), it is easy to arrange equivalence classes for two or  
399 more species consisting of disjoint subsets, in which proportional population growth rates are not all zero. We call  
400 these *alternative equivalent states*. Such states may look very different in terms of abundances and physicochemical  
401 variables. Since it is easy to construct these geometrically, we suggest that they will be common in nature.

402 A key theme in ecosystem ecology has been to identify regularities in ecosystem development (e.g. Odum, 1969).  
403 A visual representation of patterns in growth space for a particular ecosystem (e.g. Figure 4) is purely exploratory.  
404 Nevertheless, there is the potential to identify general patterns of dynamics in growth space, based on the axiomatic  
405 approach to population dynamics advocated by Lotka (1956, pp. 57-66), Hutchinson (1978, pp. 1-5), and Cropp  
406 and Norbury (2012, 2015), among others. However, the structural difference between dynamics of equivalence  
407 classes of ecosystem states and the dynamics of ecosystems has an important bearing on the kinds of regularities  
408 that a given mechanism can generate. For example, an influential, if controversial, idea in ecosystem ecology is that  
409 ecosystems are shaped by natural selection on the ability to capture energy (Lotka, 1922). Lotka's argument relies  
410 on the assumption that increased energy capture increases proportional population growth rate, and can therefore  
411 be subject to natural selection. Lotka proposed that such selection on energy capture leads to maximization of  
412 biomass and energy flow at the ecosystem level. However, unpredictable external events may generate variation  
413 within equivalence classes, which is invisible to natural selection. Thus, natural selection cannot lead to regularities  
414 by eliminating such variation over time. We argued above that equivalence classes may be disjoint, containing  
415 ecosystems with quite different physicochemical properties. If there are regularities at the ecosystem level, either  
416 they must be at the level of equivalence classes, or they must be generated by some mechanism other than natural  
417 selection. Stability selection is one such mechanism (Borrelli et al., 2015). Stability selection acts "without 'seeing'  
418 the local environment" (Damuth and Ginzburg, 2018), or in other words, it does not act via proportional population  
419 growth rates. It is therefore unlinked from the equivalence classes of an ecosystem, and may have the potential to  
420 generate regularities even within equivalence classes.

421 In conclusion, we distinguish between the view of ecosystems taken by an external observer, with the ability to  
422 study whatever they like, and an organism in an ecosystem, for whom proportional population growth rates are the

423 only relevant aspect of ecosystem state. This distinction leads to major differences in the approach that should be  
424 taken to comparative studies of ecosystems: ecologists should focus on patterns in proportional population growth  
425 rates, rather than patterns in other properties of ecosystems. Scalar summaries of these patterns such as size  
426 change and shape change are already available, but can sometimes conceal important differences among ecosystem  
427 states. The idea of alternative stable states can be generalized to equivalent ecosystem states with very different  
428 physicochemical properties. Finally, since natural selection acts only on proportional population growth rates,  
429 regularities in other aspects of ecosystem structure may not be explicable by natural selection.

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493 **Appendix A. Can dynamics on  $R$  have the same structure as dynamics on  $S$ ?**

494 To determine whether dynamics on  $R$  (as experienced by organisms in the ecosystem) can have the same structure  
 495 as dynamics on  $S$  (visible to an external observer), we must first specify an endomap  $\beta$  on  $R$  that describes these  
 496 dynamics. A natural choice for  $\beta$  is a map taking  $r(s)$  to  $(r \circ \alpha)(s)$  (the outcome of dynamics on ecosystems, mapped  
 497 to  $R$ ), if such a map exists. Thus, suppose that  $z \in r(S)$ . To get from  $z = r(s)$  to  $\beta(z) = (r \circ \alpha)(s)$ , we have to first  
 498 go back to  $S$ , then apply  $\alpha$  and finally go from the result of this to  $R$ . The function  $r$  is not in general one-one, so  
 499 it will not in general have a retraction  $\tilde{r}$  that undoes it in the sense that  $\tilde{r} \circ r = 1_S$  (Lawvere and Schanuel, 2009,  
 500 p. 53). However, we can construct the function

$$r' : r(S) \rightarrow S$$

$$z \mapsto s^*,$$

501 where  $s^*$  is an arbitrary representative of the set  $\{s \in S : r(s) = z\}$ . Then if the function  $r \circ \alpha \circ r'$  exists, it is the  
 502 natural choice for  $\beta$  on  $r(S)$ . For elements of  $R$  outside the image set of  $S$  under  $r$ , we can define  $\beta$  in an arbitrary  
 503 way, say  $\beta = 1_R$ .

504 It is clear that we will not always be able to construct  $\beta$  in this way. In fact, if we cannot, then there is no  
 505 endomap on  $R$  such that  $r$  is a structure-preserving map from  $S$  to  $R$ .

506 **Theorem 1.** *The map  $r : S \rightarrow R$  can be a structure-preserving map if and only if the endomap  $\alpha$  on  $S$  satisfies*  
 507 *the condition that*

$$s \sim s' \implies \alpha(s) \sim \alpha(s') \quad \forall s, s' \in S. \quad (\text{A.1})$$

508

509 *Proof.* First, we show that if Condition A.1 holds, then the endomap  $\beta$  on  $R$  is structure-preserving. If the condition  
 510 holds, then by the definition of  $\sim$ ,  $s \sim s' \implies (r \circ \alpha)(s) = (r \circ \alpha)(s')$ . Then

$$\beta : R \rightarrow R$$

$$z \mapsto \begin{cases} (r \circ \alpha)(s) & \text{if } z \in r(S), \\ z & \text{otherwise} \end{cases} \quad (\text{A.2})$$

511 is a valid endomap on  $R$  (because it has domain and codomain  $R$ , and associates a single element of its codomain  
 512 with each element of its domain). It also satisfies  $r \circ \alpha = \beta \circ r$ , and is therefore structure-preserving.

513 Now, we show that if Condition A.1 does not hold, then there cannot be any endomap on  $R$  such that  $r$  is  
 514 structure-preserving. Suppose that there exist  $s, s' \in S$  such that  $s \sim s'$ , but  $\alpha(s) \not\sim \alpha(s')$ . Then by the definition  
 515 of  $\sim$ ,  $r(s) = r(s')$ , but  $(r \circ \alpha)(s) \neq (r \circ \alpha)(s')$ . There cannot be any function  $\gamma$  that maps  $r(s) = r(s')$  to both  
 516  $(r \circ \alpha)(s)$  and  $(r \circ \alpha)(s') \neq (r \circ \alpha)(s)$  when these elements are distinct, and hence it is not possible to satisfy  
 517  $r \circ \alpha = \gamma \circ r$ .

518 We have shown that if Condition A.1 holds, then there is a natural choice of endomap  $\beta$  such that  $r$  is a  
 519 structure-preserving map from  $S$  to  $R$ , and that if it does not hold, then there can be no such map.  $\square$

520 Theorem 1 makes intuitive sense. Condition A.1 says that for dynamics on the set of equivalence classes to  
 521 preserve the structure in ecosystem dynamics, the ecosystem dynamics must not separate equivalence classes. For  
 522 example, in Figure A.1a, the structure of  $\alpha$  can be preserved by  $r$ , for the natural choice of the endomap  $\beta$  on  $R$   
 523 described in Appendix A, because  $\alpha$  keeps members of equivalence classes together. In contrast, in Figure A.1b,

524 the structure of  $\alpha$  cannot be preserved by  $r$  because  $s$  and  $s'$  are in the same equivalence class but are mapped by  
 525  $\alpha$  to different equivalence classes. Condition A.1 is somewhat analogous to the condition under which a function of  
 526 a Markov chain will be Markovian (Burke and Rosenblatt, 1958).

527 To find examples of endomaps  $\alpha$  satisfying Condition A.1, we first construct a function  $\phi : S \rightarrow S$  such that  
 528  $s \sim s' \iff \phi(s) = \phi(s')$ .

529 **Lemma 1.** *Let  $\phi$  be the function*

$$\begin{aligned} \phi : S &\rightarrow S \\ s &\mapsto s^* \text{ such that } s \sim s^*, \end{aligned}$$

530 *i.e.  $s^*$  is any fixed representative of the equivalence class of  $s$  on  $S$ . Then  $s \sim s' \iff \phi(s) = \phi(s')$ .*

531 *Proof.* If  $s \sim s'$ , then  $\phi(s) = \phi(s') = s^*$ . Conversely, if  $s \not\sim s'$ , then  $\phi(s) = s^*$ , but  $\phi(s') \neq s^*$ , since an equivalence  
 532 relation on  $S$  partitions  $S$  (Halmos, 1974, p. 28), so that  $s^*$  cannot be equivalent to both  $s$  and  $s'$ .  $\square$

533 We can now rewrite Condition A.1 as

$$\phi(s) = \phi(s') \implies (\phi \circ \alpha)(s) = (\phi \circ \alpha)(s') \quad \forall s, s' \in S. \tag{A.3}$$

534 This is simply an alternative way of saying that the endomap  $\alpha$  on  $S$  must not separate members of equivalence  
 535 classes.

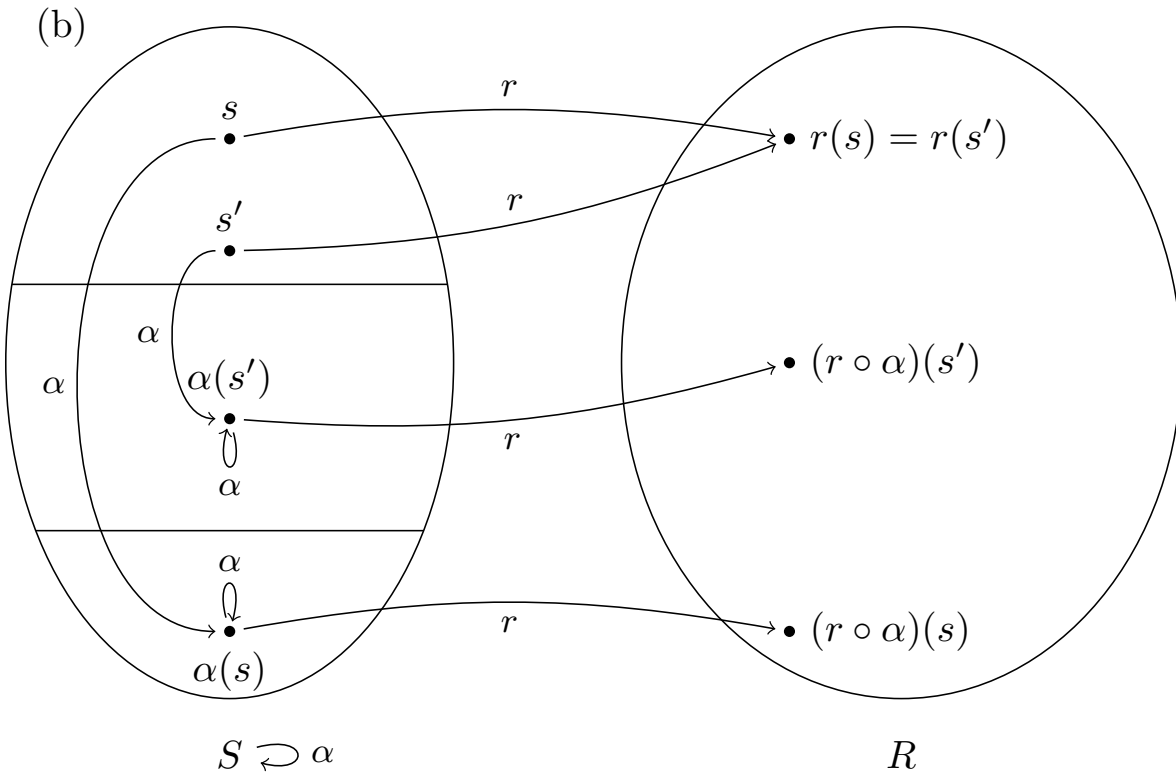
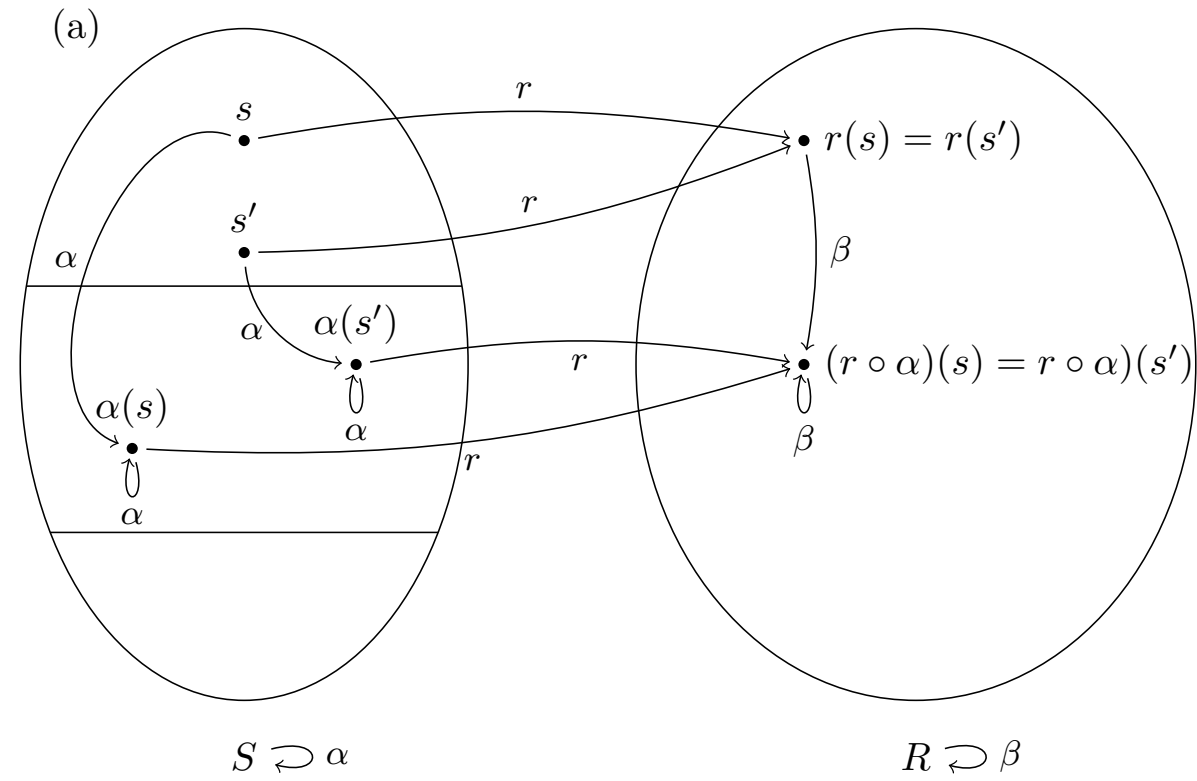


Figure A.1: Examples of endomaps  $\alpha$  on a set of ecosystem states  $S$  for which  $r$  is (a) or is not (b) a map in the category of sets with endomaps. In each case, the horizontal divisions in  $S$  represent equivalence classes, with all points in a class mapped by  $r$  to the same point in growth space  $R$ .

536 **Appendix B. Frequency-dependent dynamics**

537 Suppose that proportional population growth rates in a closed system depend only on  $\mathbf{x}$  through the relative  
 538 abundances  $\boldsymbol{\rho} = (\sum_{i=1}^n x_i)^{-1} \mathbf{x}$ . Let  $\boldsymbol{\psi}$  be a function from  $\mathbb{S}^{n-1} \times \mathbb{R}_{\geq 0}$  (where the simplex  $\mathbb{S}^{n-1}$  contains the relative  
 539 abundances, and  $\mathbb{R}_{\geq 0}$  contains a time difference) to  $\mathbb{R}^n$ . Then for some time interval  $\Delta t$ , ecosystem dynamics  $\alpha$  are  
 540 given by

$$\alpha : S \rightarrow S,$$

$$(\Omega, \mathbf{x}, \mathbf{y}) \mapsto (\Omega, \mathbf{x} \odot \boldsymbol{\psi}(\boldsymbol{\rho}, \Delta t), \mathbf{y}),$$

541 where  $\odot$  denotes the elementwise (Hadamard) product. Hence for any given set of relative abundances  $\boldsymbol{\rho}$ , all  
 542 ecosystems with abundances of the form  $c\boldsymbol{\rho}$  for some positive number  $c$  map to ecosystems with abundances of the  
 543 form  $c\mathbf{x} \odot \boldsymbol{\psi}(\boldsymbol{\rho}, \Delta t)$ . Also, for each species  $i$ ,

$$r_i(s) = \lim_{\Delta t \rightarrow 0} \frac{\psi_i(\boldsymbol{\rho}, \Delta t) - 1}{\Delta t},$$

544 which depends on  $\mathbf{x}$  only through  $\boldsymbol{\rho}$ . Thus all ecosystems with abundances of the form  $c\boldsymbol{\rho}$ , for fixed  $\boldsymbol{\rho}$ , will be in an  
 545 equivalence class, and will be mapped to the same new equivalence class by  $\alpha$ .