Mixotrophy: the missing link in consumer-resource based ecologies

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Abstract

The classical separate treatments of competition and predation, and difficulties in providing a sensible theoretical basis for mutualism, attest to the inability of traditional models to provide a synthesising framework for trophic interactions, a fundamental component of ecology. Recent approaches to food web modelling have focused on consumer-resource interactions. We construct a unifying theoretical framework to explicitly represent finite resources for each population using Lotka-Volterra (LV) equations. We show that mixotrophy, a ubiquitous trophic interaction in marine plankton, provides the key to developing a synthesis of the various ways of making a living. This framework also facilitates an explicit redefinition of facultative mutualism, illuminating the over-simplification of the traditional definition.

We demonstrate a continuum between types of trophic interactions: populations can smoothly evolve through these types without losing stable coexistence. This provides a theoretical basis for the evolution of trophic interactions from autotrophy through mixotrophy/mutualism to heterotrophy.

Introduction

Increasing evidence that population interactions such as mixotrophy and mutualism dominate interactions in marine (Flynn et al., 2013) and terrestrial (Boucher, 1985; Stachowicz, 2001; Husa and Goodrich-Blair, 2013) ecosystems respectively points to a need to develop a robust theoretical basis to understand how these interactions influence the dynamics of food webs.

While competition and predation interactions have attracted substantial attention from theorists for over ninety years, the theory underpinning several key ways of making a living, such as mutualism and mixotrophy, has not kept up with research in other areas. Texts on mathematical

and theoretical ecology typically treat competition and predation in detail, but are testament to the lack of theoretical understanding of mutualism and mixotrophy. For example, the text ‘Elements of Mathematical Ecology’ (Kot, 2001) in the 130 page section ‘Interacting Populations’, devotes 54 pages to predator-prey interactions and 22 pages to competition interactions, but only 11 pages to the mathematics of mutualism. Similarly, the text ‘Mathematical Biology’ (Murray, 2001) does not mention mixotrophy, and devotes just two pages to the mathematics of mutualism, commenting (p99) that:

“this area has not been as widely studied as the others even though its importance is comparable to that of predator-prey and competition interactions. This is in part due to the fact that simple models in the Lotka-Volterra vein give silly results.”

Murray’s comment is important because much of the basic theory underpinning current ecology has been derived from simple Lotka-Volterra type models. For them to produce ‘silly’ results suggests that the assumptions about the mechanisms used to construct the standard Lotka-Volterra models of mutualism are deficient, or perhaps that these models are too simple to allow nebulous interactions such as mutualism. The standard Lotka-Volterra models are used in ecological theory as heuristic models, in which the interactions between populations are crudely classified into positive, zero or negative impacts. Such crude assumptions lead to equally crude results, and suggest that a more sophisticated theoretical basis is required, even for simple Lotka-Volterra type models.

We propose a new framework for considering trophic interactions in a consumer-resource approach based on the idea of explicit representation of limiting resources. Although consumer-resource approaches are not new, we believe that ours is the first that places explicit requirements on the behaviour of populations when their resources are at the extremes of feast

(when the entire world is their food) and famine (when their resource is zero). An advantage of this framework is that it simplifies the mathematical analysis of the systems, defines a closed state space that contains all realistic behaviours of the system, and facilitates the definition of trophic profiles, and hence interactions, that heretofore have been qualitative. This approach requires that populations be measured in a common currency, typically that of a limiting nutrient. We recognise that different nutrients may limit production in real ecosystems at different times, and that it is conceivable that two nutrients may simultaneously constrain production. For clarity of discussion, here we consider only the case of a single limiting nutrient that we use as a common currency to measure all populations. We synthesise a simplified version of the Conservative Normal (CN) framework developed by Cropp and Norbury (2012b, c) with a standard Lotka-Volterra (LV) model to develop mass-conservative LVCN systems. Every population in these systems has an explicit, finite resource that allows different ways of making a living to be explicitly defined. The framework also allows previously nebulous concepts, such as indirect benefits obtained from mutualist interactions, to be quantified.

It has long been recognised that mutualism is ubiquitous in terrestrial ecosystems (Boucher, 1985), and it has recently become evident that mixotrophy is a similarly ubiquitous trophic interaction in the marine environment (Hartmann et al., 2012; Flynn et al., 2013). A better understanding is sought of mutualism and mixotrophy, and the demand for ever more complex and realistic ecosystem models to address issues such as the impacts of climate change, argues for a more rigorous theoretical basis to support ecosystem modeling (Mitra et al., 2014). We need models to understand the robustness and global stability properties of these complex systems in the sense of understanding whether species will go extinct, how community structure and/or succession might change, and whether any species will dominate the biomass (Cropp and

Norbury, 2012a). This paper presents a theoretical framework that synthesises new and existing ideas, and focuses on LVCN models to show these ideas in their simplest setting. We then apply this approach to a mutualism/parasitism transition model as an example of its use to test the ecological validity of models. We set out mathematical rules in the section Theoretical Framework that capture key properties of real ecosystems and use these to identify parameter profiles in the section of that name that define each population's trophic role. These explicit profiles allow us to examine a suite of trophic interactions (see section of that name) and allow us to define trophic transitions that synthesise previously disparate trophic interactions into a smooth spectrum. Some of these trophic transitions have been demonstrated previously for particular definitions of interactions for particular nonlinear models, and where transitions occurred at particular parameter values (Holland and DeAngelis, 2009). A key advance of our work is that it demonstrates robust transitions between trophic states in simple, heuristic LVCN systems that are associated with changes in the signs of specific interaction parameters. We also note the similarity between mixotrophy and facultative mutualism (and speculate on the representation of obligate mutualism) and finish with an example of how the mathematical rules of the CN framework may be used to identify models that have unrealistic properties and hence produce questionable behaviours.

The Theoretical Framework for LVCN Systems

The Conservative Normal (CN) framework captures fundamental ecological properties of living systems with mathematical rules. These rules formalise basic ecological concepts, principally that all organisms have to consume resources to survive, and that these resources are finite. The rules precisely define computer simulation programs and ensure that they are consistent with basic biophysical properties. Conservation of the mass of a limiting nutrient is fundamental to

the CN framework, but is a requirement considered unrealistic by some ecologists, who argue that no real ecological system exactly conserves mass. While this may be technically correct (although it is easy to define ecological domains for which conservation of mass of the limiting nutrient is a very accurate approximation) we draw analogy with the common assumption of linearity. Although it is similarly argued that no real ecological system has exactly linear processes, the simplifying assumption of linearity has led to substantial advances in theoretical ecology, as it has in other fields. We also note the current trend to conducting marine plankton ecosystem and biogeochemical research in large mesocosms that are closed to fluxes of nutrients (Riebesell et al., 2013) provides data to explicitly test predictions made using the CN framework. A detailed description of the CN framework has been published elsewhere (Cropp and Norbury, 2012b), so here we just present the essence of the framework sufficient to support the Lotka-Volterra (LV) analysis in this paper.

LVCN systems are Lotka-Volterra systems (that is, systems with a linear equation for each per capita population growth rate function f_i) that are modified to include a limiting nutrient and comply with the CN Rules below for ecological verisimilitude. We present the LVCN framework for a general n population Lotka-Volterra system of the form:

$$\dot{x}_i = x_i f_i(x_1, x_2, \dots, x_n) = x_i \left(r_i - \sum_{j=1}^n a_{ij} x_j \right), \quad i = 1, 2, \dots, n, \quad (1)$$

where the constants r_i, a_{ij} include all relevant ecosystem parameters and determine the actual forms of the life functions f_i . The coefficients r_i capture how the populations x_i interact directly with the pool of inorganic nutrient, which, as we show below, is implicit in (1). For autotrophs, which utilise inorganic nutrient to grow, the r_i represent the net interaction,

131 colloquially births minus linear deaths. For non-autotrophs, which cannot grow on inorganic
 132 nutrient, the r_i represent just linear mortality processes, and hence $r_i < 0$ for these populations.
 133 The a_{ij} describe how the populations interact, that is, the effect each population has on every
 134 other population, including itself.

135 ***CN Rule 0: How we Measure the System***

136 We assume each interacting population is sufficiently large in number (millions, billions,...) that
 137 we can ignore the typical individual and instead define a measure of the population mass in the
 138 isolated physical volume (for example, a mesocosm) that the ecosystem occupies. At time zero (
 139 $t = 0$) we measure the amount of the limiting nutrient in each living population $\hat{x}_i$ present in the
 140 ecosystem, together with the amount of inorganic (dead) nutrient $\hat{N}$ available to those n
 141 interacting populations:

$$142 \quad \hat{x}_1 + \hat{x}_2 + \dots + \hat{x}_n + \hat{N} = \hat{N}_T . \quad (2)$$

143 We then scale the measurements $\hat{x}_i$, $\hat{N}$ by the total measure of nutrient $\hat{N}_T$ that is cycling in the
 144 system, so that these scaled measurements x_i are fractions of the total nutrient in the system:

$$145 \quad x_1(0) + x_2(0) + \dots + x_n(0) + N(0) = 1 , \quad (3)$$

146 with $0 < x_i(0)$, $N(0) < 1$. Each living population $x_i(t)$ is now measured in terms of the fraction
 147 (of the total amount of cycling nutrient) that is bound into the living tissues of the individuals of
 148 that population. The amount of available inorganic nutrient $N(t)$ is also expressed as a fraction
 149 of the total cycling nutrient. We may recover the actual biomass of each population via
 150 stoichiometry.

151 **CN Rule 1: How Living Populations Change**

152 The per capita population growth rates are independent of the way in which we measure the
153 living populations, and satisfy:

154
$$\frac{1}{x_i} \frac{dx_i}{dt} = \hat{f}_i(x_1, x_2, \dots, x_n; N) . \quad (4)$$

155 The life functions $\hat{f}_i$ describe how each population grows (or dies) dependent on
156 interactions with the other populations in the system and with inorganic nutrient. The $\hat{f}_i$
157 implicitly include parameters that quantify the rates of environmental interactions, so that
158 for instance solar irradiance and ocean acidity may be included in the parameters.

159 **CN Rule 2: Conservation of Nutrient Mass**

160 We make the assumption that there is no population migration or nutrient flow in to or out of the
161 model domain and require that the total mass of (recycling) nutrient in the model domain
162 remains constant for all time (i.e. $\hat{N}_T$ is constant). The living population fractions $x_i(t)$ and the
163 inorganic nutrient fraction $N(t)$ then satisfy a conservation of total nutrient mass constraint for
164 all time $t > 0$:

165
$$x_1(t) + x_2(t) + \dots + x_n(t) + N(t) = 1 . \quad (5)$$

166 This fundamental constraint allows us to eliminate $N(t)$ from the living population equations
167 $\hat{f}_i(x_1, \dots, x_n; 1 - \sum x_i) \equiv f_i(x_1, \dots, x_n)$ so that (4) may be written in the LV form (1), for $x_i(t) > 0$.
168 Once all the living populations are known from solving (1) we can explicitly calculate the
169 amount of $N(t)$ from (5). The elimination of an explicit differential equation for inorganic

nutrient means that all the equations in the model have the same (Kolmogorov) form (1), which simplifies the analysis of the model, such as in showing that if $x_i(0)$ is positive then $x_i(t)$ is positive for all time $t > 0$.

Comparing (4) and (1), each population in an LVCN model that can utilise inorganic nutrient to grow has its interaction parameters partitioned into direct and indirect effects:

$$\dot{x}_i = x_i \left(r_i N - \sum_{j=1}^n \hat{a}_{ij} x_j \right) = x_i \left(r_i \left(1 - \sum_{j=1}^n x_j \right) - \sum_{j=1}^n \hat{a}_{ij} x_j \right) = x_i \left(r_i - \sum_{j=1}^n a_{ij} x_j \right). \quad (6)$$

All autotrophs in an LVCN system have each interaction coefficient $a_{ij} = r_i + \hat{a}_{ij}$ partitioned, where r_i represents the indirect, exploitation competition effect for limiting nutrient and $\hat{a}_{ij}$ represents the direct interaction effect.

The world's resources are finite, and this is particularly relevant to marine plankton models. It is well known that phytoplankton use up the entire available inorganic nutrient (commonly nitrogen) in the ocean mixed layer during summer blooms, and we ensure that our ecosystem model has realistic behaviour when the key limiting inorganic nutrient runs out. Equation (5) allows us to define a lid by $\{x_1 + x_2 + \dots + x_n = 1\}$ (i.e. $N = 0$), on the model's state space $x_i > 0$ for all i . The lid completes the closure of the state space in which reasonable model solutions exist, and hence defines the ecospace E (see Fig. 1) as the unit simplex:

$$E \equiv \{0 < x_i, 0 < x_1 + x_2 + \dots + x_n < 1\}. \quad (7)$$

CN Rule 3: Resources and Normal Ecosystems

All living populations x_j require food to survive and grow. This food may be inorganic nutrient in the cases of autotrophs, or prey (i.e. other living organisms) in the cases of non-autotrophs.

190 One population (for example, a mixotroph or an omnivore) may have several resources which we
 191 sum and consider as a single resource (i.e. $R_j = \sum_p x_p$ for population j). Here x_p are the
 192 resources, where $p \in \{0, 1, 2, \dots, n\}$ is a vector that identifies the resource populations. Note that
 193 the number of elements of p must be greater than or equal to one, and that $x_0 \equiv N$. These
 194 resources R_j are finite and limit the growth of population x_j when they become depleted; hence
 195 resources should be explicitly represented for every population in ecosystem models, as
 196 otherwise a population could have unlimited growth (Cropp and Norbury, 2012b). We define
 197 two basic criteria that a living population (measured by x_j) must comply with: when its
 198 resources are maximal ($R_j = 1$, a feast), the population x_j must be able to grow; and when there
 199 is no resource available ($R_j = 0$, a famine), the population x_j must die, where we recall that the
 200 resource for each population may be comprised of multiple populations. This means that each
 201 life function f_j must satisfy the natural resource constraints:

$$f_j \Big|_{R_j=1} > 0 > f_j \Big|_{R_j=0} . \quad (8)$$

203 Note: for non-autotroph populations x_j , that feed on another population x_i , $R_j = x_i$ where $i < j$
 204 - conventionally, the populations are numbered from the lowest trophic level to the highest. In
 205 the case of autotrophs, which feed on inorganic nutrient N , their resource is $R_j = x_0 \equiv N$. This
 206 resource is a maximum at the origin of E (where all living populations are zero and $N = 1$) and
 207 a minimum on the lid of E , which is defined by $N = 0$ in (5).

208 The food web description of the ecology implies that each population x_j has a resource R_j
 209 (which may be one or more of $N, x_1, x_2, \dots, x_{j-1}$). This means that for each x_j , we can divide the
 210 boundary of E into regions of “famine”, where $R_j = 0$ (this includes the vertex of E where $x_j = 1$
 211) and regions of “feast”, where $R_j = 1$ (which includes the vertices of E where x_j feeds).
 212 Condition (8), with (1), means that each population must have just one zero isosurface (defined
 213 by $f_j = 0$) that divides the ecospace into two parts – a part in which the population can grow and
 214 a part in which the population declines (Fig. 1). Equilibrium points, where all populations remain
 215 constant, occur where the zero isosurfaces intersect. Note that each population also has a second
 216 zero isosurface (defined by $x_j = 0$) which is part the boundary of E ; that is, the co-ordinate
 217 boundaries of the ecospace (edges, faces, etc) are also zero isosurfaces for the appropriate
 218 populations. Boundary equilibrium points are defined by at least one of the $x_i = 0$, and the local
 219 stability of these points is shown in Fig. 2 by open (unstable) or closed (stable) circles. Note that
 220 for planar life functions f_i increases monotonically as the population moves from famine to feast
 221 on straight lines across the ecospace E .

222 **Consistency Condition: the Lid and the Ecospace**

223 The lid condition guarantees that solutions $\{x_1(t), x_2(t), \dots, x_n(t)\}$ of equations (1) which
 224 start in E do not leave E through the lid, i.e. that $N(t)$ remains positive, and that mass
 225 conservation is physically sensible. Differentiating equation (5) and using (1) provides a lid
 226 condition:

$$\frac{dN}{dt} = -\frac{dx_1}{dt} - \frac{dx_2}{dt} \dots - \frac{dx_n}{dt} = -\sum_{i=1}^n x_i f_i = -\sum_{i=1}^n x_i \left(r_i - \sum_{j=1}^n a_{ij} x_j \right) > 0 \quad \text{when } N = 0, \quad (9)$$

ensuring $N \geq 0$ for all time (in fact, $N(t) > 0$ when $N(0) > 0$). Equation (9) is not necessarily satisfied for all parameter values for LV systems (1), and must be checked for each LV system. The lid condition provides some generic conditions on the parameters. For instance, $\dot{N} > 0$ holds at each vertex of the lid $x_k = 1$ with $x_i = 0$ for $i \neq k$ in (1) (this is a requirement for the model to be in CN form), which implies:

$$a_{kk} > r_k \quad \text{for each } k \text{ where } 1 \leq k \leq n. \quad (10)$$

The lid condition therefore places the constraint on every population, irrespective of its trophic interactions or level, that the dependence of the per capita self-regulating effect of its increasing population size must exceed its maximum per capita growth rate. Whenever a population has a net positive linear growth term $r_i x_i$ (i.e. all autotrophs) then its quadratic mortality term $-a_{ii} x_i^2$ must have $a_{ii} > r_i > 0$. Autotroph populations must then have carrying capacity-like terms, whereas predator populations with $r_i < 0$ need only have $a_{ii} > r_i$, and may have $a_{ii} = 0$.

240

241 **Parameter Profiles**

The explicit representation of the resources for each population in an LVCN system allows each population to be characterised by how it makes a living. This is reflected in relationships between parameters that allow us to identify a ‘parameter profile’ for each population type based on its trophic interactions.

246 **Autotrophs**

247 Autotrophs utilise inorganic nutrient N as their food source. The conservation of mass criterion
 248 $N = 1 - x_1 - x_2 - \dots - x_n$ indicates that $N = 1$ at the origin of E where all $x_i = 0$ and is zero on the
 249 lid of E where $x_1 + x_2 + \dots + x_n = 1$. The sign conditions (8) place constraints on the sign of the f_i
 250 at these extremes (Fig. 1). The maximum resource condition for an autotroph x_i stipulates:

$$251 \quad f_i \Big|_{N=1} > 0 \Rightarrow r_i > 0 . \quad (11)$$

252 The zero resource condition evaluated at each of the lid vertices $x_j = 1$ stipulates:

$$253 \quad f_i \Big|_{N=0} < 0 \Rightarrow r_i < a_{ij}, \quad j = 1, 2, \dots, n , \quad (12)$$

254 which as a bonus ensures that autotrophs (always) satisfy the lid condition (9) and the generic
 255 autotroph profile (10).

256 Summarising (11) and (12) reveals that an autotroph population x_i will always have the
 257 parameter profile:

$$258 \quad 0 < r_i < a_{ij}, \quad j = 1, 2, \dots, n . \quad (13)$$

259 We recall from (6) that when a population consumes inorganic nutrient the interaction
 260 coefficients $a_{ij} = r_i + \hat{a}_{ij}$ may be partitioned into an indirect effect (r_i) and a direct effect ($\hat{a}_{ij}$).
 261 Here, the r_i component of the a_{ij} , represents the effect on x_i of indirect competition for
 262 resources from itself and other populations, that is, that resources are not available to fuel x_i 's
 263 growth because they are already bound into the living tissues of itself or other populations. The
 264 remaining fractions of the interaction terms $\hat{a}_{ij}$ then represent the direct effects of competition or
 265 transfer of mass by predation.

266 **Green mixotrophs**

267 An autotroph population that habitually also ingests living organic matter may be classified as a
 268 mixotroph; we define a green mixotroph to be an organism that obtains more benefit from
 269 photosynthesis than it does from preying on other organisms. For a mixotroph population x_i
 270 feeding on a prey population x_h this changes the autotroph parameter profile (13) by requiring
 271 that $f_i|_{x_h=1} > 0$ in addition to (11), giving $f_i|_{0 \leq x_h \leq 1} > 0$ when $x_j = 0$ for $j \neq h$. Green mixotrophy
 272 is defined by $r_i = f_i|_{N=1} > f_i|_{x_h=1} = r_i - a_{ih} > 0$, providing the condition for green mixotrophs x_i
 273 with prey x_h :

$$274 \quad 0 < a_{ih} < r_i \Leftrightarrow |\hat{a}_{ih}| < r_i \quad \text{and} \quad \hat{a}_{ih} < 0. \quad (14)$$

275 The zero resource condition provides the parameter constraint (12) for $j \neq h$. Combining (12)
 276 and (14) gives the parameter profile for a green mixotroph x_i with resources N and x_h :

$$277 \quad 0 < a_{ih} < r_i < a_{ij} \Leftrightarrow -r_i < \hat{a}_{ih} < 0 < r_i < a_{ij} \quad \text{for} \quad j = 1, 2, \dots, n \quad \text{but} \quad j \neq h. \quad (15)$$

278

279 **Red mixotrophs**

280 We call a mixotroph population x_i that grows mostly by feeding on another population x_h (i.e.

281 $r_i - a_{ih} = f_i|_{x_h=1} > f_i|_{N=1} = r_i > 0 \Rightarrow a_{ih} < 0$) a ‘red’ mixotroph. It has the parameter profile:

$$282 \quad a_{ih} < 0 < r_i < a_{ij} \quad \text{for} \quad j = 1, 2, \dots, n \quad \text{but} \quad j \neq h. \quad (16)$$

283 Note that (16) implies that $|\hat{a}_{ih}| > |r_i|$ for red mixotrophs.

284 **Heterotrophs**

285 A heterotroph (predator) population grows by feeding on one or more other populations; in the
 286 latter case the predator is called an omnivore. For a heterotroph population x_i growing by
 287 feeding on a single population x_h the maximum resource condition, evaluated where its prey is
 288 maximal, gives the parameter constraint:

$$289 \quad f_i \Big|_{x_h=1} = r_i - a_{ih} > 0 \Rightarrow r_i > a_{ih} . \quad (17)$$

290 The zero resource condition applied at the origin of E provides the parameter constraint

$$291 \quad f_i \Big|_{N=1} = r_i < 0 , \quad (18)$$

292 and applied at the other vertices of E where $x_h = 0$ provides the constraints:

$$293 \quad f_i \Big|_{x_j=1} = r_i - a_{ij} < 0 \Rightarrow r_i < a_{ij} \quad \text{for } j \neq h . \quad (19)$$

294 A heterotroph population x_i with prey x_h therefore has the parameter profile:

$$295 \quad a_{ih} < r_i < 0 \quad \text{and} \quad r_i < a_{ij} \quad \text{for } j = 1, 2, \dots, n \quad \text{but } j \neq h . \quad (20)$$

296 The parameter profile for heterotrophs defined by the LVCN framework does not completely
 297 define predation, as this involves the parameter profile of the prey population as well. We
 298 impose the condition that the predator x_i has an interaction with its prey x_h such that

$$299 \quad a_{ih} < 0 < a_{hi} , \text{ indicating a direct transfer of mass from the prey to the predator, and } |a_{ih}| < |a_{hi}| ,$$

300 reflecting that the predator is not perfectly efficient at converting prey biomass into predator
 301 biomass. Note that when the prey population is an autotroph the direct and indirect effects must
 302 be identified (recall that in the case of an autotroph x_h , $a_{hi} = r_h + \hat{a}_{hi}$) as the efficiency of the

relationship between the predator and prey involves only the direct interaction. The magnitude condition for a heterotroph x_i feeding on an autotroph x_h is then $|a_{ih}| < |\hat{a}_{hi}|$. Omnivory is a general class of trophic interactions that includes mixotrophy (above) and heterotrophy where the predator has multiple prey. Parameter profiles for omnivores may be inferred from those of mixotrophs and heterotrophs. The examination of omnivorous heterotrophs in LVCN systems requires at least three populations, and will not be considered further here, but is present in the example considered in the Application section.

Mutualism

Mutualist populations obtain a net benefit from an interacting mutualist population, but do not necessarily directly consume it. The benefits may be in the form of resources such as food, nutrients or shelter, or benefits imparted by services such as pollination, seed dispersal or protection. In LVCN systems a benefit is represented explicitly by an increase in the fraction of limiting nutrient incorporated into the mutualist population. An indirect benefit acquired by a mutualist in an LVCN system is indistinguishable in the population's parameter profile from a direct benefit acquired by a heterotroph. Mutualism is differentiated from predation only when the parameter profile of the interacting population is considered. The parameter profile for an autotroph mutualist x_i interacting with its benefactor x_h is therefore the same as for a mixotroph:

$$0 < a_{ih} < r_i < a_{ij} \quad \text{or} \quad a_{ih} < 0 < r_i < a_{ij} \quad \text{for} \quad j = 1, 2, \dots, n; \quad j \neq h, \quad (21)$$

and for a heterotroph mutualist is the same as that for a predator:

$$a_{ih} < r_i < 0 \quad \text{and} \quad r_i < a_{ij} \quad \text{for} \quad j = 1, 2, \dots, n; \quad j \neq h. \quad (22)$$

324 Mutualism is differentiated from predation since the direct interaction coefficients for both
 325 populations may be positive ($\hat{a}_{ij} > 0$ and $\hat{a}_{ji} > 0$ for autotrophs (recall equation (6)) or $a_{ij} > 0$
 326 and $a_{ji} > 0$ for non-autotrophs) and the gain by the mutualist exceeds the loss from the prey (
 327 $-a_{ji} > \hat{a}_{ij}$ for autotroph prey or $-a_{ji} > a_{ij}$ for heterotroph prey). Rather than a (net) direct transfer
 328 of mass from the prey to the predator as occurs for predation, the fact that both interactions are
 329 positive indicates that the benefit obtained by mutualists (in LVCN systems) results from a net
 330 transfer of mass from the nutrient pool. The examination of mutualist heterotrophs in LVCN
 331 systems requires at least three populations, and will not be considered in this paper.

332 **Trophic Interactions**

333 The following discussion of trophic interactions considers a two-population LVCN system:

$$334 \quad \begin{aligned} \dot{x}_1 &= x_1 (r_1 - a_{11}x_1 - a_{12}x_2) \\ \dot{x}_2 &= x_2 (r_2 - a_{21}x_1 - a_{22}x_2) \end{aligned} \quad (23)$$

335 In considering these two-population LVCN models, we recall that only parameter sets for which
 336 the CN Lid Condition ($\dot{N} > 0$ when $N = 0$), explicitly:

$$337 \quad -x_1 (r_1 - a_{11}x_1 - a_{12}x_2) - x_2 (r_2 - a_{21}x_1 - a_{22}x_2) > 0 \quad \text{with } x_2 = 1 - x_1 \quad \forall 0 \leq x_1 \leq 1, \quad (24)$$

338 is always satisfied, provide ecologically realistic models. We shall limit our discussion to cases
 339 where the lid condition is satisfied, and note that violations to the lid condition may place
 340 constraints on realistic parameter sets or models. The properties of the coexistence equilibrium
 341 point $\{x_1^*, x_2^*\}$, located at:

$$342 \quad x_1^* = \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}; \quad x_2^* = \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}}, \quad (25)$$

and whether it exists as a stable point in E , will be relevant to the discussion. (Note that the location of this stable point in E does not guarantee that the lid condition is satisfied.) The set of model trophic interactions that maintain a stable interior point in E and satisfy the lid condition is shown in Fig. 2. Some valid “interactions”, such as competing autotrophs in which one autotroph always goes extinct, are not shown but are well known in the literature and will not be considered in detail here.

Competing Autotrophs

We first consider competing autotrophs, where from (13), $0 < r_1 < a_{11}, a_{12}$ and $0 < r_2 < a_{21}, a_{22}$. A well-known result in theoretical ecology is that in cases of strong inter-population competition ($a_{11}a_{22} \leq a_{12}a_{21}$) the populations are subject to competitive exclusion and either x_1 or x_2 dominates depending on the initial conditions. In this case the coexistence point exists in E but is unstable. If $a_{11}a_{22} = a_{12}a_{21}$ the coexistence point does not exist in E and the relative magnitudes of r_1 and r_2 determine the outcomes of the competition in what has come to be described as R^* theory (Tilman, 2007). When $a_{11}a_{22} > a_{12}a_{21}$ the coexistence point exists stably in E and the previously competitive exclusion system becomes a system with coexisting competitors (Fig. 2a).

Note that the CN lid condition is satisfied for an LVCN system containing only autotrophs, therefore, every parameter set that complies with the generic parameter constraints for autotrophs (13) will produce a realistic autotroph competition LVCN system. Competing autotroph systems have the following general properties that competitive exclusion occurs if $a_{11}a_{22} < a_{12}a_{21}$; the R^* case occurs and x_1 wins if $r_1/r_2 > a_{12}/a_{22}$ and $r_1/r_2 > a_{11}/a_{21}$ while x_2 wins if $r_1/r_2 < a_{12}/a_{22}$ and

364 $r_1/r_2 < a_{11}/a_{21}$; and stable coexistence at $\{x_1^*, x_2^*\}$ in E is ensured if $a_{11}a_{22} > a_{12}a_{21}$. In this case,
 365 the CN theoretical framework produces exactly the classical competition results.

366 ***Autotroph (Prey) – Heterotroph (Predator)***

367 We now consider a predator-prey system, where the prey x_1 is an autotroph with the parameter
 368 profile $0 < r_1 < a_{11}, a_{12}$ and the predator has the profile $a_{21} < r_2 < 0$ and $r_2 < a_{22}$. Fig. 2g shows
 369 that if $r_1/a_{11} > r_2/a_{21}$ the f_1 and f_2 zero isoclines of the prey and predator respectively will
 370 intersect and that, as x_1 is an autotroph, the coexistence point will exist in E . Note $a_{22} > 0$ in Fig.
 371 2g, but $a_{22} < 0$ leads to identical conditions on coexistence. We note that $a_{22} < 0$ implies
 372 population autocatalysis, where an increase in the population's size improves conditions for
 373 itself, but we will not consider this case further in this work.

374 LVCN predator-prey (heterotroph-autotroph) systems have the general property that the
 375 populations coexist at (x_1^*, x_2^*) in E if $r_1/a_{11} > r_2/a_{21}$. Note that unlike the autotroph competition
 376 case, the lid condition is not always satisfied under the parameter profiles for an autotroph and a
 377 predator. Even if the coexistence point exists in E the vector field for the system may allow
 378 trajectories to exit E and hence violate ecological realism. The lid condition for a heterotroph-
 379 autotroph predator-prey pair is modified from the general two-population lid condition (24) to
 380 differentiate between direct and indirect interaction effects:

$$\begin{aligned}
 & -x_1 \left(r_1 - (r_1 + \hat{a}_{11})x_1 - (r_1 + \hat{a}_{12})x_2 \right) - x_2 \left(r_2 - a_{21}x_1 - a_{22}x_2 \right) > 0 \\
 381 \quad & \Rightarrow -x_1 \left(r_1 (1 - x_1 - x_2) - \hat{a}_{11}x_1 - \hat{a}_{12}x_2 \right) - x_2 \left(r_2 - a_{21}x_1 - a_{22}x_2 \right) > 0. \quad (26) \\
 & \Rightarrow \hat{a}_{11}x_1^2 - r_2x_2 + (\hat{a}_{12} + a_{21})x_1x_2 + a_{22}x_2^2 > 0
 \end{aligned}$$

If we take the common case for a heterotroph (i.e. $a_{22} > 0$) and impose less than 100% efficiency on the heterotroph (i.e. $-a_{21} < \hat{a}_{12}$) then the parameter profiles for an autotroph (13) and a heterotroph (20), ensure that every term in the final line of (26) is positive and the lid condition is always satisfied. However, for systems with more than two trophic levels the lid condition must be explicitly checked for each parameter set to ensure the model is ecologically valid.

Competing Green Mixotrophs

Autotrophs, by (13), have $r_i < a_{ij}$. When an autotroph, say x_2 , changes its feeding behaviour by, perhaps opportunistically, ingesting x_1 , a_{21} becomes less than r_2 (specifically $\hat{a}_{21} < 0$) and x_2 becomes a green mixotroph, defined by the parameter profile $0 < a_{21} < r_2 < a_{22}$ (Fig. 2b). The change in sign of $\hat{a}_{21}$ is apparent in Fig. 2b as the f_2 zero isocline extending outside the lid before it crosses the x_1 axis. This is ecologically realistic: it does not necessarily violate the lid condition, but unlike pure autotroph interactions, the lid condition could be violated in autotroph-mixotroph systems.

Fig. 2b can be reached by a single parameter perturbation from the coexisting autotroph competitors, each feeding solely on inorganic nutrient, shown in Fig. 2a. Fig. 2d shows that x_1 may also adapt by ingesting x_2 , thereby reducing a_{12} , the strength of its net interaction with x_2 . This is again a single parameter perturbation from Fig. 2b. In both Figs. 2b and d, the populations have changed the signs of their direct interaction coefficients $\hat{a}_{12}$ and $\hat{a}_{21}$ while keeping the overall interaction coefficients a_{12} and a_{21} positive.

We see from Fig. 2b, d that competing autotrophs/green mixotrophs will always stably coexist unless they violate the lid condition and the coexistence point exists outside E . The lid condition

403 for a green mixotroph pair is modified from the general two-population lid condition (24) to
 404 differentiate between direct and indirect interaction effects:

$$\begin{aligned}
 & -x_1 \left(r_1 - (r_1 + \hat{a}_{11})x_1 - (r_1 + \hat{a}_{12})x_2 \right) - x_2 \left(r_2 - (r_2 + \hat{a}_{21})x_1 - (r_2 + \hat{a}_{22})x_2 \right) > 0 \\
 405 \quad & \Rightarrow -x_1 \left(r_1 (1 - x_1 - x_2) - \hat{a}_{11}x_1 - \hat{a}_{12}x_2 \right) - x_2 \left(r_2 (1 - x_1 - x_2) - \hat{a}_{21}x_1 - \hat{a}_{22}x_2 \right) > 0. \quad (27) \\
 & \Rightarrow \hat{a}_{11}x_1^2 + (\hat{a}_{12} + \hat{a}_{21})x_1x_2 + \hat{a}_{22}x_2^2 > 0
 \end{aligned}$$

406 As $\hat{a}_{11}$ and $\hat{a}_{22}$ are positive and $\hat{a}_{12}$ and $\hat{a}_{21}$ are negative for green mixotrophs it is possible for
 407 some parameter combinations to violate the lid condition, and hence the lid condition must be
 408 numerically checked for every parameter combination for green mixotroph systems.

409 ***Competing Red Mixotrophs***

410 When a green mixotroph x_2 that preferred photosynthesising to grazing on x_1 (Fig. 2b) changes
 411 its feeding preference so that its maximum per capita rate of grazing on x_1 exceeds its maximum
 412 rate of photosynthesis, $\hat{a}_{21}$ decreases further so that $a_{21} < 0$ and x_2 becomes a red mixotroph
 413 (Fig. 2c). This is evident in Fig. 2b and c by the f_2 zero isocline changing from a negative slope
 414 to a positive slope. The total interaction $a_{21} < 0$ means that the direct benefit $\hat{a}_{21}$ that x_2 obtains
 415 by feeding on x_1 exceeds the detrimental indirect effect of x_1 on x_2 due to its sequestering
 416 nutrient that reduces the amount available to x_2 for growth.

417 Fig. 2e shows a green mixotroph x_1 coexisting with a red mixotroph x_2 . This state may be
 418 reached by a single parameter perturbation from an autotroph interacting with a red mixotroph
 419 (Fig. 2c) or from two interacting green mixotrophs (Fig. 2d). Each mixotroph feeds on inorganic
 420 nutrient and the other population, but x_1 mostly photosynthesises while x_2 mostly feeds on x_1 .
 421 Fig. 2f shows coexisting red mixotrophs. In this case, both x_1 and x_2 have adapted by reducing
 422 the overall interaction coefficients a_{12} and a_{21} to below zero, indicating that the direct benefits

received by the presence of the other population ($\hat{a}_{12}$ and $\hat{a}_{21}$) exceed the cost from indirect competition for limited inorganic nutrient (r_1 and r_2).

LVCN systems of competing mixotrophs, irrespective of whether they are green or red or any combination thereof, have the general property that they always have a stable coexistence point with $x_1^*, x_2^* > 0$ and that the populations stably coexist in E if the parameter values are such that (x_1^*, x_2^*) lies in E (Fig. 2d, e and f). This general result is consistent with the results of specific modelling studies, for example Crane and Grover (2010) and Jost et al. (2004), that predict that mixotrophy enhances stable coexistence of multiple populations across trophic levels. Note that the lid condition (27) must be numerically evaluated for each parameter set for systems containing green and/or red mixotrophs.

Creation of a new trophic level

A population may change from an autotroph to a green mixotroph to a red mixotroph by a smooth change in its interaction coefficient, with definitions changing at the key transitions where the direct interaction coefficient $\hat{a}_{ij}$ changes sign (autotroph to green mixotroph) and where the overall interaction coefficient a_{ij} changes sign (green to red mixotroph). We now consider the implications of smooth changes in the direct nutrient interaction coefficient r_i .

The above cases for x_i an autotroph, a green mixotroph or a red mixotroph had $r_i > 0$, so that x_i utilised inorganic nutrient for growth. As a red mixotroph becomes increasingly dependent on predation r_i reduces until when $r_i < 0$ the red mixotroph ceases autotrophy and becomes a pure heterotroph. This transition is apparent in Fig. 2g, h and i as the f_2 zero isocline sliding down the x_2 axis until its intercept with the x_2 axis is negative. This transition changes the red mixotroph

parameter profile $a_{21} < 0 < r_2 < a_{22}$ into a predator parameter profile $a_{21} < r_2 < 0 < a_{22}$, a restricted case of the parameter profile imposed by the CN Rules (20).

The same parameter condition that allows heterotrophs to survive on autotrophs ($r_1/a_{11} > r_2/a_{21}$, Fig. 2g) ensures coexistence between a green or red mixotroph and a predator (Fig. 2h, i). In all cases, these interactions result in stable coexistence points in E unless the lid condition is violated and ecological realism is lost.

Trophic transitions

The ways of making a living and the interactions discussed above and shown in Fig. 2 have a common feature – they all have a stable coexistence equilibrium point in the ecospace E . Recall that we consider only ecologically realistic cases where the lid condition is not violated, evidenced in Fig. 2 by all the vectors on the lid pointing into E . These trophic interactions form a continuum from competition to predation that may be smoothly transitioned by single parameter variations that maintain coexisting interacting populations. Smooth reductions in the direct interaction coefficients $\hat{a}_{12}$ and $\hat{a}_{21}$, and the overall interaction coefficients a_{12} and a_{21} , induce movements from left to right in Fig. 2, with key transitions occurring when $\hat{a}_{12}$ and $\hat{a}_{21}$ change sign, and when a_{12} and a_{21} change sign. The transition from autotroph to green mixotroph represents the development of an ability to consume other living matter, for example by phagotrophy. The transition from green mixotroph to red mixotroph reflects a changing food specialisation, from growing mostly by photosynthesising to growing mostly by predating on other organisms. These transitions all occur “within” a trophic level.

A new trophic level is created when the coefficient representing direct interaction with inorganic nutrient r_i changes sign. In Fig. 2 we only considered a change in sign of r_2 as two-population

LVCN systems must have at least one autotroph. A change of sign of r_2 appears in Fig. 2 as vertical transitions that create a new trophic level, when x_2 loses the ability to grow on inorganic nutrient and becomes a pure heterotroph. We note that the classic rubric for competitive coexistence, that “intraspecific competition exceeds interspecific competition” (i.e. $a_{11}a_{22} > a_{12}a_{21}$), holds in all cases in Fig. 2. The cases where this does not hold are well known and do not have coexisting populations, and hence are omitted from Fig. 2.

Mutualist interactions

The usual definition for a mutualist pair x_1 and x_2 in classical Lotka-Volterra models has (in our notation) $a_{12} < 0$ and $a_{21} < 0$ so that each mutualist population has a net positive effect on the other. The classic examples of mutualism in simple Lotka-Volterra models differentiate between facultative and obligate mutualism, for each of which weak and strong interactions are considered. The classic distinction between weak and strong mutualism is borrowed from competition theory, with mutualism described as weak if $a_{11}a_{22} > a_{12}a_{21}$ and strong if $a_{11}a_{22} < a_{12}a_{21}$.

The result of the classical analysis of mutualism is the, rather unsatisfactory and counter-intuitive, rubric that only weak facultative mutualists can coexist (for example, Pastor, 2008). The standard Lotka-Volterra models predict that strong facultative mutualists will have infinitely large populations, weak obligate mutualists will always both go extinct, and strong obligate mutualists will either both go extinct or both have infinitely large populations. The definition of a bounded ecospace that contains all possible ecologically reasonable solutions to LVCN systems indicates that the CN framework can identify mutualism models that violate the CN framework’s requirement that benefits obtained via mutualism must be ecologically reasonable.

Facultative Mutualism

Facultative mutualism is defined in the classical Lotka-Volterra models (for example, Pastor, 2008) by parameter profiles equivalent to $a_{12} < 0 < r_1 < a_{11}$ and $a_{21} < 0 < r_2 < a_{22}$ in our notation, the profile we have attributed to red mixotrophs. Further, the classical interaction diagram shown for weak facultative mutualism is qualitatively identical to our diagram for interacting red mixotrophs (Fig. 2f) and has a stable coexistence point in E . The classical case for strong facultative mutualism predicts that no ecologically realistic solutions can be obtained as the parameter profiles ensure that the coexistence point (25) cannot exist in E .

The LVCN system (23) provides a much more satisfactory insight into weak and strong facultative mutualism. We recall from our earlier discussion of (6) that the net interaction coefficients a_{ij} can be decomposed into direct and indirect components $a_{ij} = r_i + \hat{a}_{ij}$. This facilitates us differentiating facultative mutualism in LVCN systems by defining weak facultative mutualism in an LVCN system as the case when the direct interactions are positive but the overall interaction remains negative (i.e. $\hat{a}_{12} < 0$ and $\hat{a}_{21} < 0$ but $a_{12} > 0$ and $a_{21} > 0$, equivalent to a pair of green mixotrophs, Fig. 2d) and strong facultative mutualism as the case when the overall interactions are positive (i.e. $a_{12} < 0$ and $a_{21} < 0$, equivalent to a pair of red mixotrophs, Fig. 2f). This definition clearly delineates weak facultative mutualists as those populations that gain more benefit from other sources than from their mutualist, and strong facultative mutualists as those that gain more from their benefactor than from other sources.

507 We may now define parameter profiles for weak and strong facultative mutualists as being
508 identical to the parameter profiles of green mixotrophs ($0 < a_{ik} < r_i < a_{ij}$ for $j = 1, 2, \dots, n; j \neq k$,
509 $\hat{a}_{ik} < 0$), and red mixotrophs ($a_{ik} < 0 < r_i < a_{ij}$ for $j = 1, 2, \dots, n; j \neq k$) respectively.

510 **Obligate Mutualism**

511 The classical case for obligate mutualism is defined by the parameter profiles $r_1 < 0$, $r_2 < 0$,
512 $K_1 < 0$ and $K_2 < 0$ (for example see Pastor, 2008) equivalent to $a_{12} < r_1 < 0 < a_{11}$ and
513 $a_{21} < r_2 < 0 < a_{22}$ in our notation. The classic case for weak obligate mutualism never allows a
514 coexistence point in E . The strong case does, but it is unstable and the lid condition is always
515 violated, indicating an ecologically invalid model.

516 The classic parameter profiles for obligate mutualism are identical to those of two interacting
517 populations of heterotrophs in the LVCN framework. These systems cannot be represented in a
518 two-population LVCN framework suggesting higher dimension LVCN systems are required to
519 represent obligate mutualism. It may be the case that nonlinear interactions, as proposed by
520 Holland and DeAngelis (2010), or density dependent growth parameters as suggested by Graves
521 et al. (2006), are fundamental to obligate mutualism.

522 Note that the lid condition of the LVCN framework provides a constraint on the magnitude of
523 benefits that a mutualist may obtain from an interaction with its benefactor, and that these
524 constraints apply to both “weak” and “strong” mutualist interactions. We now investigate the
525 role of the lid condition in this context.

Applications in Ecology

Kolmogorov (1936) made arguably the first, and perhaps the only, attempt to develop a set of rules that ensured that ecosystem models produced ecologically sensible solutions. Kolmogorov considered a generic Lotka-Volterra predator-prey model and articulated nine specific criteria that ensured that both populations existed and that solutions remained bounded. Kolmogorov's paper initially had little impact, with Resigno and Richardson's (1967) paper providing one of the few applications. May (1973) popularised the work with ecologists and provided more detailed ecological interpretations of Kolmogorov's criteria. He also noted that they contained a minor inconsistency in that Kolmogorov's third and fourth criteria required the net growth rate of the predator to simultaneously strictly increase and strictly decrease as its population size changed when the prey population was exactly zero. May and some that applied Kolmogorov's criteria (for example Upadhyay and Rai (2001)) considered it reasonable to relax these strictly positive/negative criteria to allow equality and facilitate application of the criteria to ensure that a model was "biologically meaningful" .

Despite the pragmatic resolution of the inconsistency, Kolmogorov's criteria were little used in theoretical ecology or ecological modelling to ensure ecological validity, perhaps because of their unwieldy application. Assessment of a two-population model required nine criteria to be tested, and applied to predator-prey interactions, a small subset of possible population interactions. The work was never extended to higher dimensions, possibly due to the explosion in the number of criteria that appeared inevitable, and no other criteria that could be used to evaluate the ecological veracity of a model appear to have been published until recent work by Cropp and Norbury (2012a; 2012b; 2014), which this paper synthesises, extends and applies.

548 The CN framework described above has many applications in theoretical ecology, one of which
 549 we demonstrate in our synthesis of the ways of making a living in ecology. However, a
 550 pragmatic application of the framework is an objective test that allows the ecological veracity of
 551 a model to be evaluated. Unlike Kolmogorov's criteria the CN rules are easily extended to
 552 systems with many populations and trophic interactions, providing a pragmatic tool for assessing
 553 ecological systems of any complexity. Note that the CN Rules evaluate the ecological validity of
 554 a model; they do not, as Kolmogorov's criteria do, ensure the existence of an internal
 555 equilibrium point where all populations coexist. Whilst this is a straightforward additional
 556 constraint for two-populations, as demonstrated by Kolmogorov's ninth criterion that ensures the
 557 intersection of the predator and prey zero isoclines, it becomes much more complicated as
 558 populations are added to a system, and for systems with interactions other than just predator-
 559 prey.

560 Predator-prey interactions are unique in consumer-resource based Lotka-Volterra and LVCN
 561 systems in that they involve an explicit transfer of mass from the prey x_i (in LVCN notation
 562 $\hat{a}_{ij}x_ix_j$) to the predator x_j ($a_{ji}x_ix_j$), usually with a fraction of the mass lost by the prey (
 563 $(\hat{a}_{ij} + a_{ji})x_ix_j$, recall that $a_{ji} < 0$ in such cases) going to the inorganic nutrient pool as respiration
 564 and similar processes. However, when $-a_{ji} > \hat{a}_{ij}$ the interaction becomes mutualistic as the
 565 predator can derive more benefit (biomass) from the prey than the prey loses via predation. In
 566 this case, as in all other interactions such as mixotrophy, mutualism and competition, interactions
 567 between populations involve quantifiable flows of mass via the nutrient pool. LVCN systems
 568 represent these flows and the nutrient pool explicitly (although they are implicit in the model

equations) and hence are able to articulate constraints on, for example, mutualist interactions that are somewhat nebulous in other modelling frameworks.

We demonstrate the application of the CN Rules to test ecological veracity by briefly considering the model of Neuhauser and Fargione (2004). This model considered a three-population system comprising a host (H), a symbiont (P) and a parasite (Q) and was used to examine the transition from mutualism to parasitism in plant-mycorrhizae interactions across gradients of soil fertility. The model used a carrying capacity (K) to constrain the growth of the host, to facilitate representation of the benefit accrued by the host as a result of the presence of the symbiont, and to provide a surrogate for soil fertility:

$$\begin{aligned}
 \frac{dH}{dt} &= H \left(r - \frac{rH}{K + \gamma P} - a_1 P - a_2 Q \right) \\
 \frac{dP}{dt} &= P \left(-d_1 + b_1 H - d_1 e_1 P - c_1 d_1 Q \right) \\
 \frac{dQ}{dt} &= Q \left(-d_2 + b_2 H - c_2 d_2 P - d_2 e_2 Q \right)
 \end{aligned} \tag{28}$$

Neuhauser and Fargione (2004) do not state that mass is conserved in their model, however, they do assume that the host dynamics in the absence of the symbiont follow logistic growth. The assumption of logistic growth of the lowest trophic level in a three-population Lotka-Volterra model is equivalent to assuming that mass is conserved (Cropp and Norbury, 2012b), hence, we may recast (28) into pseudo-LVCN form (pseudo in the sense that it is Lotka-Volterra only when $\varepsilon = 0$):

$$\begin{aligned}
 \dot{x}_1 &= x_1 f_1(x_1, x_2, x_3) = x_1 \left(r_1 - \frac{a_{11}}{1 + \varepsilon x_2} x_1 - a_{12} x_2 - a_{13} x_3 \right) \\
 \dot{x}_2 &= x_2 f_2(x_1, x_2, x_3) = x_2 \left(r_2 - a_{21} x_1 - a_{22} x_2 - a_{23} x_3 \right) \\
 \dot{x}_3 &= x_3 f_3(x_1, x_2, x_3) = x_3 \left(r_3 - a_{31} x_1 - a_{32} x_2 - a_{33} x_3 \right)
 \end{aligned} \tag{29}$$

586 where we have used the definitions:

$$\begin{aligned}
 \tilde{x}_1 &= H, & \tilde{r}_1 &= r, & \tilde{a}_{11} &= \frac{r}{K}, & \tilde{a}_{12} &= a_1, & \tilde{a}_{13} &= a_2, \\
 \tilde{x}_2 &= P, & \tilde{r}_2 &= -d_1, & \tilde{a}_{21} &= -b_1, & \tilde{a}_{22} &= d_1 e_1, & \tilde{a}_{23} &= c_1 d_1, & \text{and } \tilde{\varepsilon} &= \frac{\gamma}{K}, \\
 \tilde{x}_3 &= Q, & \tilde{r}_3 &= -d_2, & \tilde{a}_{31} &= -b_2, & \tilde{a}_{32} &= c_2 d_2, & \tilde{a}_{33} &= d_2 e_2,
 \end{aligned}
 \tag{30}$$

588 and we have non-dimensionalised (29) and (30) using a characteristic time ($T = r$) and total

589 mass in the system (N_T) such that $t = \tilde{t} T$ and $x_i = \frac{\tilde{x}_i}{N_T}$. The state variables x_i in (29) are now

590 constrained so that $0 \leq x_1, x_2, x_3 \leq 1$ and $0 \leq x_1 + x_2 + x_3 \leq 1$, and the new parameters are obtained

591 from (30) using the relations $r_i = \frac{\tilde{r}_i}{T}$, $a_{ij} = \frac{\tilde{a}_{ij} N_T}{T}$ and $\varepsilon = \tilde{\varepsilon} N_T$. Applying these transformations

592 to the parameters cited for Tables 1 and 2 in Neuhauser and Fargione (2004), using the

593 maximum host growth rate $T = r = 2$ and the maximum carrying capacity $N_T = \max(K) = 20$,

594 we derive the parameter set for (29):

$$r = \begin{bmatrix} 1 \\ -0.5 \\ -0.5 \end{bmatrix} \quad A = \begin{bmatrix} a_{11} & 3 & 4 \\ -30 & 10 & a_{23} \\ -20 & 6.128 & 10 \end{bmatrix}. \tag{31}$$

596 Here, either $a_{23} = 14$, from Table 1 of Neuhauser and Fargione (2004), or $a_{23} = 16.5$, from Table

597 2. The values of a_{11} and ε depend on the value of K , which Neuhauser and Fargione vary

598 between 2 and 20 to represent low and high soil fertility respectively. This leads to values of a_{11}

599 and ε that vary between $a_{11} = 10$ and $\varepsilon = 50$ (for $K = 2$) to values of $a_{11} = 1$ and $\varepsilon = 5$ (for

600 $K = 20$).

601 We first examine the parameter profiles for the populations. Neuhauser and Fargione consider
 602 the host x_1 a plant, which in an LVCN system has the parameter profile that defines an
 603 autotroph, $0 < r_1 < a_{11}, a_{12}, a_{13}$. Applying CN Rule 3 at the origin (maximum resource) and the
 604 vertices of the lid (minimum resource) for (29) results in this profile for $K < 20$. However, the
 605 f_1 zero isosurface is not a plane in this pseudo-LVCN system so we further need to check that
 606 $f_1 < 0$ everywhere on the lid. We provide a graphical example of the isosurfaces and the lid in
 607 Fig. 3 to demonstrate the importance of CN Rule 3 and the lid condition. The parameter profiles
 608 for x_2 and x_3 ($a_{21} < r_2 < 0 < a_{22}, a_{23}$ and $a_{31} < r_3 < 0 < a_{32}, a_{33}$) are consistent with
 609 predator/obligate mutualist/parasite roles, with $-a_{21} > \hat{a}_{12}$ and $-a_{31} > \hat{a}_{13}$ indicating that both
 610 populations receive mutualist benefits from x_1 (that is, they acquire nutrient mass as a result of
 611 the interaction in excess of that obtained by direct predation).
 612 Violation of the lid condition of the CN framework, a result of its explicit resource limitation,
 613 provides an objective criterion to determine when the benefit obtained by mutualists is excessive
 614 and unrealistic. This appears to be the case in the Neuhauser and Fargione model, where the
 615 parameters describing the indirect benefits accrued by the mutualists (a_{21} and a_{31}) due to the
 616 presence of x_1 are an order of magnitude larger than the direct losses from x_1 ($\hat{a}_{12}$ and $\hat{a}_{13}$).
 617 Although in this case complying with the lid condition cannot be achieved simply by reducing
 618 a_{21} and a_{31} (other parameters need to be changed as well), it is worth examining the role of a_{21}
 619 and a_{31} in the behaviour of the Neuhauser and Fargione model, as these are not identified as
 620 important parameters in the paper, and a reason for their inordinate magnitude is not provided.

621 The examples of switching from mutualism to parasitism provided by Neuhauser and Fargione
622 (Tables 1 and 2) rely on changes in the abilities of the mutualist and parasite to invade the
623 ecospace. These are controlled by the competition eigenvalues of the populations at the boundary
624 equilibrium points where they are zero (Cropp and Norbury, 2012c), the mutualist invasion point
625 $\{x_{1-M}^*, 0, x_{3-M}^*\}$ and the parasite invasion point $\{x_{1-P}^*, x_{2-P}^*, 0\}$. The competition eigenvalues at
626 these points are respectively:

$$\begin{aligned}
\lambda_{x_2} &= f_2 \Big|_{\{x_{1-M}^*, 0, x_{3-M}^*\}} = r_2 - a_{21}x_{1-M}^* - a_{23}x_{3-M}^* \\
\lambda_{x_3} &= f_3 \Big|_{\{x_{1-P}^*, x_{2-P}^*, 0\}} = r_3 - a_{31}x_{1-P}^* - a_{32}x_{2-P}^*
\end{aligned} \tag{32}$$

628 The reason for the large values for a_{21} and a_{31} (and indeed a_{23} and a_{32} which are also very
629 large) is now apparent as the boundary equilibrium points (especially $\{x_{1-P}^*, x_{2-P}^*, 0\}$) are only
630 weakly sensitive to variations in K (Tables 1 and 2 in Neuhauser and Fargione (2004)). The large
631 magnitude of these parameters serves to amplify the changes in the locations of the boundary
632 equilibrium points and to change the signs of the competition eigenvalues, and hence the abilities
633 of the zero populations to invade.

634 This analysis suggests that it is unlikely that parameter sets might be found that can
635 simultaneously reproduce transitions from mutualism to parasitism while satisfying the CN
636 criteria for basic ecological realism. It is not the objective of this article to investigate
637 mutualist/parasite transitions, so we leave as an open question whether this renders Neuhauser
638 and Fargione's conclusions invalid, or merely unlikely.

Discussion

We have presented a consumer-resource framework in which every population has an explicit, finite limiting resource. This CN ecological framework conserves a finite total nutrient mass (C), and has per capita growth rates that must be negative when no resource is available, and increase as more resource becomes available to the population; per capita growth rates must be positive when maximum resources are available (N). We define a simple Lotka-Volterra model within this framework (to create an LVCN system) that provides a simple ecologically rigorous model with which to examine trophic interactions. The representation of (mixed) populations as fractions of the total amount of recycling nutrient means that the ecospace E representation of Fig. 1 is now very convenient, with ecosystem life histories now naturally lying in E when the rules are satisfied.

We introduce mixotrophy to the usual autotrophy and heterotrophy that have provided much of the theory of population interactions, and derive explicit population parameter profiles from the LVCN framework that define ways of making a living. We show that mixotrophs can be naturally classified as either green, when they mostly grow by consuming inorganic nutrient, or red, when they mostly grow by consuming another population. Again, the use of E allows a natural graphical definition of these new population interactions, and examples are shown in Figs. 2 and 3.

The inclusion of mixotrophy to the standard cases of autotrophy and heterotrophy reveals a continuous spectrum of trophic interactions that links competition in autotrophs to predator – prey interactions. A key attribute of this spectrum is that it is possible to transition through all trophic interactions in a series of smooth, one-parameter variations that maintain a stable coexistence equilibrium point inside the ecologically realistic state space E . Autotrophs may

662 smoothly and stably transition into green mixotrophs by developing phagotrophy, and into red
663 mixotrophs by preferentially feeding on other organisms. Red mixotrophs transition into
664 heterotrophs by losing their autotrophic capability. These population transitions and interactions
665 are summarised in Fig. 2.

666 The use of mixotrophs as an intermediate and bridging population type provides a smooth
667 sequence of stable population interaction models for marine and aquatic systems. The
668 correspondence between our profiles for mixotrophs and the classical profiles for mutualists
669 suggests that the LVCN models provide a useful theoretical framework to consider facultative
670 mutualism within terrestrial ecosystems. Consequently, we suggest that facultative mutualists
671 may similarly provide a smooth sequence of stable population interaction models for terrestrial
672 systems.

673 Facultative mutualist populations defined within the LVCN framework have identical population
674 parameter profiles to mixotrophs. The LVCN framework suggests a new clear distinction
675 between weak⁺ and strong⁺ facultative mixotrophy that provides facultative mutualism with a
676 more satisfactory theoretical basis where both weak⁺ and strong⁺ facultative mutualists may
677 stably coexist. The CN lid condition limits the benefit that mutualists may accrue from
678 interactions to ecologically sensible levels, that have been breached in the mutualist/parasite
679 transition model of Neuhauser and Fargione (2004), rendering this example ecologically
680 untenable.

681 The two-population LVCN system does not, however, provide a useful description of obligate
682 mutualism. The traditional population parameter profile for obligate mutualists is identical to that
683 of heterotrophs, and it is not possible to define a two-population model in the LVCN framework

that consists only of interacting heterotrophs. Whether obligate mutualism requires nonlinearity or can be adequately represented by a three-population LVCN system will be addressed in future work.

The afore-mentioned clearly describes the efficacy of the CN framework in synthesising previously disparate aspects of ecological interactions into a continuous, simply transitioned spectrum from competition through mixotrophy and mutualism to predator-prey interactions – see Fig. 2. We also demonstrated the efficacy of the CN Rules in identifying models that transgress fundamental ecological principles. In some cases, this merely means that the parameter set used to demonstrate a particular result needs to be selected more judiciously, but in some cases may render conclusions drawn from a model invalid. We are not aware of another ecological modelling framework that allows such a pragmatic and efficient identification of ecologically inconsistent models.

Conclusion

This work presents a unifying framework for the study of trophic interactions within a Lotka-Volterra setup. In doing so, it considers two ubiquitous interactions of theoretical ecology for which there is a paucity of theoretical understanding: mixotrophy, the dominant interaction among plankton in the oceans (Flynn et al., 2013), and mutualism, the dominant interaction on land (Hussa and Goodrich-Blair, 2013). Fig. 1 summarises a representation of an ecology using as variables fractions of the total recycling, limiting nutrient in the ecology. This ecospace allows a simple and natural definition of mixotrophic and mutualist populations and interactions. The LVCN framework facilitates a precise definition of mixotrophy and illuminates refinements of the traditional models of mutualism. It suggests a new, explicit distinction between weak and

706 strong facultative mutualism, and predicts that both stably exist; this implies that the classic
707 definition of strong facultative mutualism (for example, Pastor, 2008, p171) is deficient.

708 The CN framework also has pragmatic applications in ecology to identify models that are
709 ecologically inconsistent. Kolmogorov (1936) made the first attempt to constrain solutions to
710 Lotka-Volterra models to maintain ecological validity, but his nine conditions had an internal
711 inconsistency, were unwieldy to implement for two populations, and became much more
712 unwieldy as the number of populations increased. The CN framework in contrast is internally
713 consistent, has few conditions, and extends to models with many populations with little extra
714 difficulty. A further advantage of the CN framework is the lid condition that provides the
715 ultimate simple check of a model's ecological credentials. In particular, the lid condition allows
716 us to identify an ecologically invalid parameterisation for a particular set of equations that
717 otherwise satisfy conditions for ecological reasonableness. The importance of the lid condition is
718 very clearly illustrated by Neuhauser and Fargione (2004) which, in the example provided at
719 least, requires violation of the lid condition to be able to demonstrate the desired result.

720 Finally, the LVCN framework provides a theoretical basis for the evolution of populations from
721 autotrophy (including competition) through mixotrophy/mutualism to predation. Figs. 2 and 3
722 illustrate these various population interactions, together with their coexisting population states.
723 This spectrum of adaptation, via smooth single parameter variations that maintain stably
724 coexisting populations, gives the first theoretical basis to synthesise trophic interactions that have
725 historically been treated separately.

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789 **Fig. Legends**

790 FIG. 1. Resource spaces and zero isosurfaces for (a) an autotroph where x_1 feeds on inorganic
791 nutrient, and (b) a non-autotroph where x_3 feeds on x_2 .

792 FIG. 2. Heuristic diagram showing the smooth transition from a pair of coexisting competitors
793 (a) through various forms of mixotrophy (b-e) to coexisting red mixotrophs (f), all transitions
794 involving smooth variations in $\hat{a}_{12}$, $\hat{a}_{21}$, a_{12} or a_{21} . The establishment of a new trophic level is
795 shown by the transitions involving r_2 (c to g, e to h and f to i). Populations move within both
796 trophic levels by smoothly changing the magnitude and sign (positive to negative) of their inter-
797 population interaction terms ($\hat{a}_{12}$, $\hat{a}_{21}$, a_{12} and a_{21}). Populations move between trophic levels by
798 smoothly changing the sign of r_2 . During all these changes a stable coexistence equilibrium
799 point is maintained within E . The parameter changes that create each new way of making a
800 living are shown in the arrows between the relevant state spaces. Panels show the conservation of
801 mass lids (dotted lines), the zero isoclines (solid lines), the vector fields (arrows), and stable
802 (filled circles) and unstable (open circles) equilibrium points. The horizontal axes all show the
803 size of the x_1 population and the vertical axes the size of the x_2 population. The lid of the
804 ecospace in each case is shown by the dotted line extending from (1, 0) to (0, 1). The maximum
805 value on each axis is extended to 1.2 to show clearly the zero isoclines for the
806 mixotroph/mutualist cases (b-f, h, i). Note that commensal (+, 0) and amensal (-, 0) interactions
807 occur where a_{12} and a_{21} change sign: amensalism is a transition state between (b) and (c) and
808 between (d) and (e); while commensalism occurs in the transition between (e) and (f).

809 FIG 3. Zero isosurfaces (panels (a) and (c)) and vector fields (panels (b) and (d)) for the model
 810 (29) with the parameter set for Table 2 of Neuhauser and Fargione (2004) (rescaled in (31)) with
 811 $K = 2$ (panels (a) and (b)) and $K = 20$ (panels (c) and (d)). The zero isosurfaces are f_1 (blue),
 812 f_2 (black) and f_3 (green). Dots show the locations of the critical points; open dots are unstable
 813 and filled dots are stable. The point $\{x_1^*, x_2^*, 0\}$ is stable in (a) and (b) and the point $\{x_1^*, 0, x_3^*\}$ is
 814 stable in (c) and (d). The green and red lines are typical trajectories starting from different initial
 815 conditions. Note the intersection of the f_1 zero isosurface with the lid (the dotted triangle in the
 816 plane of the page) in (c) revealing violation of CN Rule 3 in the region of the lid below the
 817 intersection with the f_1 zero isosurface, where $f_1|_{R_1=0} > 0$. Violation of the lid condition is
 818 evidenced in (b) and (d) by some of the vectors on the lid pointing out of E (in the $\{x_1, x_2\}$ plane
 819 in (b) and both the $\{x_1, x_2\}$ and $\{x_1, x_3\}$ planes in (d)), and further in (d) by the green trajectory
 820 exiting E through the lid. Note that CN Rule 3 is satisfied for all populations in (a) and (b) but
 821 the lid condition is violated. This also demonstrates that the behaviour of trajectories is not a
 822 reliable indicator of whether a model is ecologically realistic.
 823

824 **Figures**

825 **Fig 1:**

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(a)

(b)

(c)

(d)

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