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**PARAMETERISING COMPETING ZOOPLANKTON FOR SURVIVAL IN
PLANKTON FUNCTIONAL TYPE MODELS**

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Parameterisation
Dynamical system
Kolmogorov system

31

32 **ABSTRACT**

33

34 Marine plankton ecosystems are an important component of biogeochemical cycling in the oceans.
35 Operational plankton functional type (PFT) models, that group plankton according to their
36 biogeochemical properties, are currently being developed to resolve biogenic gas exchange between
37 the ocean and atmosphere, and to model the lowest trophic levels in fisheries models. A
38 fundamental problem with these models is that PFTs often go extinct in computer simulations,
39 effectively removing the biogeochemical processes from the models. Cropp and Norbury (Journal
40 of Plankton Research, 31: 939-963) demonstrated that parameter combinations that allowed all
41 PFTs to stay extant for all time in stable, homogeneous environments were rare in a PFT model
42 with two competing phytoplankton and one zooplankton (NP_1P_2Z). In this paper, we examine the
43 dynamical properties of a generic predator-predator-prey PFT model, and apply the analysis
44 techniques developed by Cropp and Norbury to a simple example PFT model with one
45 phytoplankton and two zooplankton (NPZ_1Z_2) in order to explore its properties and parameter
46 space. We find that the properties of predator-predator-prey PFT systems are fundamentally
47 different from those of predator-prey-prey PFT systems. The likelihood of parameter combinations
48 for which all PFTs stay extant for all time in predator-prey-prey PFT systems depends critically on
49 the process formulations used, while the properties of co-existing zooplankton (as defined by their
50 parameter values) are quite different to those of co-existing phytoplankton.

51

52

53 **INTRODUCTION**

54

55 Plankton may have a significant influence on climate by drawing down carbon dioxide from the
56 atmosphere and sequestering it in the deep ocean, and by producing dimethylsulphide and other
57 volatile compounds that may affect cloud formation over the oceans. Plankton models that include
58 several plankton functional types (PFTs) are needed to resolve the role of plankton in
59 biogeochemical cycling, as different plankton utilise different elements in different ways (Le Quéré
60 et al. 2005). However, there has been significant debate over whether plankton ecosystems are
61 sufficiently well understood to place any reliance on the results of models that include multiple
62 PFTs (Anderson 2005, Le Quéré 2006).

63

64 A particular problem with PFT models is that when the model is solved numerically (as all but the
65 very simplest PFT models must be) it is common for PFTs to go extinct in the model simulations
66 (Cropp and Norbury 2009a). This is an undesirable outcome, as each PFT in the model is there to
67 facilitate a specific biogeochemical process, so it is a common practice to include computational
68 ‘fixes’ in PFT computer models to prevent PFTs from going extinct. However, such practices mean
69 that the PFT model that is solved on the computer is different from the PFT model that is described
70 by the equations. Cropp and Norbury (2009a) observed that this disparity meant that the computed
71 model solutions were not *bona fide* solutions of the model equations (see Terminology section
72 below for the definition of our usage). They investigated the nature and ubiquity of the parameter
73 sets required to ensure that the numerical solution of a model accurately reflected the model
74 equations rather than a model with fewer PFTs. They considered the parameterisation of a model
75 that resulted in all PFTs remaining extant for all time to be *bona fide*, and investigated the ubiquity
76 of this behaviour in a simple PFT model. They observed that over 99% of parameter sets for a
77 simple PFT model resulted in numerical solutions in which at least one PFT went extinct, and that
78 consequently *bona fide* parameter sets were rare in the parameter space of these models. They
79 subsequently developed some heuristics for the construction and parameterisation of simple PFT
80 models with competing phytoplankton (pPFTs) to ensure *bona fide* properties. We reiterate that a
81 *bona fide* PFT model is merely one for which the computed solution of a model, as defined by its
82 equations and parameterisation, maintains all PFTs extant and is therefore a faithful representation
83 of the model. The terminology does not imply that *bona fide* PFT models are better representations
84 of real ecosystems.

85

86 The problem of maintaining PFTs extant in computer simulations is consistent with much
87 ecological theory. The paradox of the plankton (Hutchinson 1961) articulates exactly this problem,
88 that models of plankton systems typically only allow one functional type to exist per resource in
89 constant homogeneous environments. Many solutions to the paradox have been proposed, and
90 include internal chaotic dynamics (Huisman and Weissing 1999), external forcing (Ebenhoh 1988),
91 spatiotemporal effects (Petrovskii et al. 2003) or interaction effects such as prey-switching by
92 predators (Krivan 2003). These solutions have proved of little use in practice, as they often rely on
93 quite special conditions (Schippers et al. 2001). Similarly, the addition of internal processes such as
94 intra-guild predation can lead to the presence of alternative stable states (Polis and Holt 1992,
95 Mylius et al. 2001) that can facilitate competitive exclusion. This raises interesting questions of the

96 nexus between model formulations that allow multiple stable states, and the ubiquity of parameter
97 sets that realise them as feasible states of the system.

98

99 The difficulty of maintaining competing PFTs extant in computer simulations, when the ecosystem
100 models are coupled to physical models of the ocean that vary in space and time, suggests that much
101 of the theory that has been developed for coexistence in variable environments provides little
102 practical benefit in simulations of life in the oceans. We shall demonstrate, however, that some of
103 the basic concepts that underpin processes such as invasion in varying environments are both
104 relevant and able to be explicitly articulated in our analyses. In particular, the concept of the ‘long-
105 term low-density growth rate’ that has been shown to be central to coexistence in a variety of
106 deterministic and stochastic ecosystem models (Ellner 1984, Chesson 1994, Law and Morton 1996,
107 Chesson 2000). This conceptual metric determines whether a species can successfully invade an
108 established ecosystem and is analogous to the crucial eigenvalues that we shall show are readily and
109 reliably obtained in analytic form for the systems we consider.

110

111 A tenet of invasion theory based on terrestrial plant communities is that positive long-term low-
112 density growth rates are only ensured by stabilising mechanisms, and that these stabilising
113 mechanisms are always based on the partitioning of a resource (Barot and Gignoux 2004). In
114 terrestrial communities, the partitioning of a resource appears to be considered synonymous with
115 variation in space and/or time (Barot and Gignoux 2004), and that the partitioning of space and time
116 supersedes all other resources (Tilman and Pacala 1993, Chesson 2000). The applicability of these
117 concepts to coexistence among plankton communities is moot, as these organisms live in
118 environments that are relatively homogeneous over the relevant short space and time scales, and
119 have limited ability to move through their environment. We shall therefore focus attention in this
120 work on alternative ways in which organisms may have positive long-term low-density growth
121 rates.

122

123 In this paper, we build on the results reported in Cropp and Norbury (2009a), hereafter referred to
124 as CN09, and consider a model with multiple zooplankton functional types (zPFTs) that is a three-
125 dimensional Kolmogorov system in a stable, homogeneous environment. Three-dimensional
126 Kolmogorov systems include a very broad class of ecosystem models, and are merely any system
127 that can be written in the following form

$$\begin{aligned}
 \mathcal{R}_1 &= f_1(u_1, u_2, u_3)u_1 \\
 \mathcal{R}_2 &= f_2(u_1, u_2, u_3)u_2 \\
 \mathcal{R}_3 &= f_3(u_1, u_2, u_3)u_3
 \end{aligned}
 \tag{1}$$

128

129 In the cases we will consider u_1 will represent a phytoplankton and u_2 and u_3 will represent
 130 zooplankton. It is debatable whether NPZ_1Z_2 systems are common in the real oceans; however, we
 131 observe that understanding the properties of subsystems can provide useful insights into the
 132 properties of more complex systems (Cropp and Norbury 2009b). They may also have direct
 133 application in so-called ‘end-to-end’ fisheries models, where multiple zPFTs (typically
 134 differentiated by size) are required to couple primary production to higher trophic levels in fisheries
 135 models (Rose et al. in press).

136

137 We will show that the functional forms used to represent mortality, and whether the zooplankton
 138 interaction includes omnivory or not, are crucial to the existence of an interior critical point, and
 139 also affect the ubiquity of parameter sets that produce *bona fide* PFT systems. We note heuristics
 140 that allow predator-predator-prey PFT models to be constructed that are *bona fide* PFT systems for
 141 all valid parameter sets; that are never *bona fide* PFT systems for any valid parameter sets; or have
 142 varying probability of being *bona fide* PFT systems.

143

144

145 METHOD

146

147 We choose the model and its parameters to ensure ecological realism under the conditions derived
 148 by Kolmogorov (1936) and explicated by May (1973) and others. We restrict our analysis to f_i that
 149 comply with Kolmogorov’s (1936) conditions as many ecosystem models in the contemporary
 150 literature have these properties (Huang and Zhu 2005). A more detailed discussion of three-
 151 dimensional Kolmogorov systems is provided in CN09.

152

153 As in CN09 we look at the particular case of a model that conserves the mass of limiting nutrient as
 154 many models applied in biological oceanography also have this property (Spitz et al. 2001, Franks
 155 2002, Vallina et al. 2008). Conservation of mass implies that the total mass of inorganic nutrient
 156 (N) present at any time is given by:

157
$$N = N_T - u_1 - u_2 - u_3 \Leftrightarrow \dot{N} = -\dot{u}_1 - \dot{u}_2 - \dot{u}_3, \quad (2)$$

158 where N_T is a constant that gives the total effective nutrient in the system and the u_i are the
 159 concentrations of the PFTs measured in this currency. We note that conservation of mass is required
 160 for many biogeochemical models to be written as Kolmogorov systems, as the nutrient equation in
 161 these models typically cannot be written in Kolmogorov form. Conservation of mass causes N to
 162 become a ‘virtual’ variable; as shown in equation (2), it allows the \dot{N} equation to be inferred from
 163 the other equations that are in Kolmogorov form.

164
 165 We scale each state variable with respect to the total nutrient (i.e. u_i/N_T), which allows us to
 166 define an ecologically feasible ‘state space’ where $0 \leq u_1, u_2, u_3 \leq 1$. We consider the critical
 167 (equilibrium) points of this system, denoted by $\{u_1^*, u_2^*, u_3^*\}$ where $\dot{u}_i = f_i u_i^* = 0$ for all time. Implicit
 168 in the rationale for constructing plankton models with more than one functional type is the
 169 assumption that, in the absence of environmental factors, an interior critical point, with
 170 $u_1^*, u_2^*, u_3^* \neq 0$, both exists and is an important determinant of the dynamics of the system.
 171 Analogously to CN09, we enquire into the nature of these interior (predator-predator-prey) critical
 172 points in systems with one autotroph and two grazers, and how this might inform the development
 173 and calibration of more complex PFT models.

174
 175 We first consider the dynamical properties of a generic three state variable Kolmogorov system
 176 (equation (1)) where the u_1 represents an autotroph (pPFT) upon which u_2 and u_3 (zPFTs) graze.
 177 The analysis of this generic system provides general results that apply to all such three variable
 178 Kolmogorov systems, irrespective of the process formulations (f_i) chosen to represent the
 179 interactions between the state variables, and independent of the parameter values used in the model.

180
 181 We consider the critical points of the system, defined by $\dot{u}_i = 0$ for all i . In Kolmogorov systems,
 182 critical points may be obtained from the isoclines in two ways for each equation, when $f_i = 0$ or
 183 when $u_i = 0$. Each critical point in a three state variable system has three eigenvalues and three
 184 associated eigenvectors. These eigenvalues and eigenvectors describe the local (Lyapunov) stability
 185 of the system in the region of each of the critical points, and together form ‘signposts’ that control
 186 the dynamics of the system. Example isoclines, critical points and eigenvectors for a predator-

187 predator-prey system are shown in Fig. 1. Some eigenvectors have been omitted for clarity; none
 188 are shown for point D but these can be inferred from those shown for B and C. Eigenvectors that
 189 always have positive eigenvalues are shown pointing away from the critical point, those that always
 190 have negative eigenvalues are shown pointing towards the critical point, and the others have
 191 double-ended arrows. Fig. 1 shows the three-dimensional state space
 192 ($\dot{x}_i = f_i(u_1, u_2, u_3)u_i$, $i = 1, 2, 3$) in which the isoclines are surfaces; where parts of the isoclines are
 193 hidden behind other isoclines they are shown by dotted lines. The dashed lines indicate the
 194 conservation of mass conditions for each face.

195

196

197 **The NPZ_1Z_2 Model**

198

199 We then consider a specific example of an NPZ_1Z_2 Kolmogorov system in order to examine the
 200 parameterisations of the system that result in *bona fide* PFT dynamics. The study system has
 201 conventional phytoplankton (P) growth on inorganic nutrient (N) balanced by zooplankton
 202 (Z_1, Z_2) grazing and linear or nonlinear mortality. The zPFTs may also include omnivory in which
 203 Z_2 predate on Z_1 .

204

205 We note that there is little consensus over the appropriate forms of the process representations in
 206 PFT models (Flynn 2003, Mitra 2009). In this paper, we choose ‘simple’ f_i that are commonly
 207 used to allow, as far as possible, for closed form analytic expressions to be found for the critical
 208 points and their eigenvalues. Even in this simple model, explicit analytic evaluation is not always
 209 possible, and we are forced to develop numerical solutions for one interior value. Analytic
 210 expressions for the key properties of PFT systems allow us to understand and predict PFT
 211 dynamics rather than merely observe them. We shall present the results of the analysis of the
 212 NPZ_1Z_2 model, equivalent to our analysis of the generic Kolmogorov system, and use these results
 213 to explore the parameter space and associated dynamical properties of this simple system.

214

215 The example NPZ_1Z_2 system is written in a currency of inorganic nutrient, with all state variables
 216 expressed as concentrations of nutrient, as described by equations (3) - (5):

$$217 \quad \dot{P} = f_P P = \left[\frac{\mu N}{N + \kappa} - \frac{\varphi_1 Z_1}{1 + \varepsilon_1 P} - \frac{\varphi_2 Z_2}{1 + \varepsilon_2 P} - \sigma P^\alpha \right] P, \quad (3)$$

$$218 \quad \dot{Z}_1 = f_{Z_1} Z_1 = \left[\frac{\varphi_1 (1 - \psi_1) P}{1 + \varepsilon_1 P} - \frac{\phi Z_2}{1 + \varepsilon Z_1} - \sigma_1 Z_1^\gamma \right] Z_1, \quad (4)$$

$$219 \quad \dot{Z}_2 = f_{Z_2} Z_2 = \left[\frac{\varphi_2 (1 - \psi_2) P}{1 + \varepsilon_2 P} + \frac{\phi (1 - \psi) Z_1}{1 + \varepsilon Z_1} - \sigma_2 Z_2^\delta \right] Z_2. \quad (5)$$

220 We check our conservation of mass criterion as per equation (2) and see that

$$221 \quad \dot{N} = \left[\sigma_1 Z_1^\gamma + \frac{\varphi_1 \psi_1 P}{1 + \varepsilon_1 P} \right] Z_1 + \left[\sigma_2 Z_2^\delta + \frac{\varphi_2 \psi_2 P}{1 + \varepsilon_2 P} + \frac{\phi \psi Z_1}{1 + \varepsilon Z_1} \right] Z_2 - \left[\frac{\mu N}{N + \kappa} - \sigma P^\alpha \right] P. \quad (6)$$

222

223 We have chosen the forms of the f_i to allow for several functional forms of grazing, omnivory and
 224 mortality to be easily considered. Phytoplankton uptake of inorganic nutrient is fixed at the
 225 Michalis-Menten functional form, but zooplankton grazing may take two forms. Setting $\varepsilon_1, \varepsilon_2, \phi = 0$
 226 in the zooplankton grazing terms allows us to represent Lotka-Volterra grazing, while Holling Type
 227 II grazing can be represented by setting $\varepsilon_1, \varepsilon_2, \phi \approx 1$. We allow $\varepsilon_1, \varepsilon_2, \phi$ to vary continuously to
 228 allow a graduation of forms, rather than switching between only two values. Omnivory of Z_2 on Z_1
 229 is allowed if $\phi \neq 0$, and is switched off if $\phi = 0$. Each of the PFT may have linear or nonlinear
 230 mortality; $\alpha, \gamma, \delta = 0$ imposes linear mortality on P, Z_1 and Z_2 respectively, while $\alpha, \gamma, \delta = 1$
 231 imposes nonlinear mortality.

232

233 There have been many functional forms proposed for nonlinear zooplankton mortality, and the
 234 impact of various forms on the dynamics of ecosystem models has been documented by several
 235 authors (Steele and Henderson 1992, Edwards and Yool 2000, Mitra 2009). We shall not
 236 investigate the effects of different nonlinear forms in this work, but shall instead demonstrate a
 237 fundamental difference in the importance of linear and nonlinear zooplankton mortality terms for
 238 the stability properties at the boundary critical points. Importantly, linear mortality terms appear as
 239 a constant in their f_i , while nonlinear mortality terms appear in their f_i as a function of Z such that

240 mortality term in the f_i goes to zero as Z goes to zero. We note that the latter is the case for all the
 241 nonlinear zooplankton mortality terms investigated by Mitra (2009), and we therefore observe that
 242 our use of quadratic zooplankton mortality, the simplest nonlinear function available, provides quite
 243 general insights.

244
 245 Different model formulations were defined by the values of $\bar{\phi}$, α , γ and δ . We shall use codes
 246 such as [0101] to denote each of these formulations, where the values are ordered $[\bar{\phi}, \alpha, \gamma, \delta]$.
 247 These codes represent the actual values used in the model except for $\bar{\phi} = 1$ which indicates that
 248 $\bar{\phi} \neq 0$ but may take other values defined by the parameter space.

249

250

251 **Parameter Space Search**

252

253 The parameter space used in CN09 was adopted as the basis for the NPZ_1Z_2 model analysis and
 254 was modified slightly to reflect that this analysis considers competing grazers rather than competing
 255 autotrophs (Table 1). The values used in CN09 were derived from typical measured values
 256 (Fenchel 1982, Moloney et al. 1986, Slagstad and Stole-Hansen 1991, Hansen et al. 1996, Muller-
 257 Niklas and Herndl 1996, Gabric et al. 1999, Gabric et al. 2001) and were non-dimensionalised prior
 258 to use by scaling time by the maximum growth rate of P (μ) and concentrations by the total
 259 nutrient (N_T). As we will be considering the effect of varying parameter values on the model
 260 dynamics, it is essential that we scale the parameters so that the influence of each parameter is
 261 revealed unequivocally. As we will evaluate each parameter set sampled for validity (see
 262 Terminology section below for the definition of our usage) we have allowed the parameter space we
 263 search to be somewhat larger than usual; this will allow for differences in the magnitude of
 264 parameter values for different process formulations.

265

266 The parameter space was searched for each model formulation using a Monte Carlo method based
 267 on uniform parameter distributions from which 10^6 randomly selected parameter sets were sampled
 268 and evaluated for validity (see definition in Terminology). Each valid parameter set was then tested
 269 for the existence and stability of an internal predator-predator-prey critical point. The same criteria
 270 used to define validity and existence/stability in CN09 are applied to this model; a parameter set is
 271 valid if all boundary critical points are ecologically realistic, Lyapunov stability criteria are used to

272 determine the stability of critical points. Analytic expressions describing these criteria for this
 273 model are given in Table 2. The general derivation of these conditions is presented in the Results,
 274 and the explicit derivation related to the model described by equations (3) - (5) is presented in the
 275 Appendix. Finally, we examined the frequency distributions of the competition and omnivory
 276 parameters of the sets that resulted in *bona fide* PFT.

277

278 We note here that the results of the parameter search will be specific to the parameter space we
 279 have defined and to the explicit model formulations that we use. Although these are quite generic
 280 examples, in that they examine both saturating and non-saturating process functions, the results will
 281 change if the parameter space is changed or the process formulations are changed. The results of the
 282 parameter space search should therefore be considered as generic examples rather than canonical
 283 systems.

284

285 **Terminology**

286

287 We will be concerned with several properties of the parameter sets that we examine. We will use
 288 the same terminology as CN09 to discuss these properties, and now define the terminology that we
 289 shall use. We shall initially classify parameter sets according to:

- 290 • their validity, that is, whether all the critical points that Kolmogorov (1936) showed must
 291 exist in the feasible region of the state space for the system to be realistic do exist, and
- 292 • we further classify valid parameter sets according to the three classes of PFT systems that
 293 they define:
 - 294 • *Bona fide* PFT systems, in which all PFT stay extant for all time. These systems have an
 295 internal critical point that has a negative real eigenvalue, and a complex conjugate pair
 296 of eigenvalues that may have positive or negative real parts;
 - 297 • Pseudo-PFT systems, in which one or the other of the competing zooplankton goes
 298 extinct depending on the initial values used. These systems have an internal critical point
 299 that has a positive real eigenvalue, and a complex conjugate pair of eigenvalues that may
 300 have positive or negative real parts;
 - 301 • Non-PFT systems, in which one or the other of the competing zooplankton goes extinct
 302 irrespective of the initial values used, that is the same zooplankton always goes extinct
 303 for each parameter set. These systems do not have an interior critical point.

304 We use the term *bona fide* quite deliberately to describe models for which the computed simulation
 305 results are *bona fide* solutions of the model described by the equations; pseudo- and non-PFT
 306 systems have computed solutions that are solutions of models with one fewer PFTs than the model
 307 described by the equations. To ensure the best available computed solutions we used an adaptive
 308 step-size 4-5th order Runge-Kutta integration scheme with absolute and relative tolerances set to
 309 machine epsilon (10^{-14}) in all our integrations. *Bona fide* does not therefore equate to realistic, and
 310 in fact we will consider both realistic and unrealistic *bona fide* models in this work and discuss the
 311 distinction between them.

312

313 **RESULTS**

314

315 We initially present the results of the analysis of the generic Kolmogorov system: (equation (1))
 316 where we define u_1 to be an autotroph and u_2 and u_3 to be its grazers. We present analytic
 317 expressions for the critical points and eigenvalues where possible, and present the generic
 318 properties of the state space described by the critical points, eigenvalues and eigenvectors
 319 graphically (Figure 1). We have labelled the critical points in Figure 1 and shall use these labels to
 320 identify the critical points and their eigenvalues in the following analysis. The values of the state
 321 variables at the critical points are denoted by the asterisk superscripts, and the critical points
 322 distinguished by their subscripts. The signs of the eigenvalues are shown where these are defined by
 323 the ecological properties of the system and always hold.

324

325 The results of this analysis are similar in many respects to the analysis of the Kolmogorov system in
 326 which u_1 and u_2 were autotrophs and u_3 was their grazer reported in CN09. The reader is therefore
 327 referred to CN09 for much of the detail, and only the differences will receive detailed treatment in
 328 this paper.

329

330

331 **Origin Critical Point (O):**

332

333 Every Kolmogorov system has a critical point at the origin (O in Fig. 1) where $u_i^* = 0$ (i.e. no life)
 334 and (usually) $f_i \neq 0$ for all i . The eigenvalues at the origin are:

335
$$\lambda_{0-1} = f_1|_O > 0, \quad (7)$$

336
$$\lambda_{0-2} = f_2|_O < 0, \quad (8)$$

337
$$\lambda_{0-3} = f_3|_O < 0, \quad (9)$$

338 where $f_i|_O$ means that the expression f_i is evaluated at the critical point O (i.e. using the values of
 339 the state variables at the critical point). The origin represents the state of the system where only
 340 inorganic nutrient exists. Near this point, autotrophs always grow and predators always die, and the
 341 point will therefore always be a saddle point. The unstable direction of the saddle (λ_{0-1}) is a result
 342 of the autotroph growing by consuming nutrient in isolation along its axis, while the stable
 343 directions (λ_{0-2} and λ_{0-3}) are those of the predators dying in the absence of prey along their axes.

344

345

346 **Prey-only Critical Point (A):**

347

348 Every model that complies with Kolmogorov's (1936) criteria will have an prey-only (autotroph)
 349 critical point in each of the predator-prey subsystems. In this case with one autotroph, the sole
 350 point, which is involved in both predator-prey subsystems, is defined by $u_1^* \neq 0, u_2^* = 0, u_3^* = 0$ (A)
 351 and is located where the $f_1 = 0$ isocline intersects the u_1 axis. The eigenvalues of this point are
 352 given by:

353
$$\lambda_{A-1} = \frac{\partial f_1}{\partial u_1} u_1|_A < 0, \quad (10)$$

354
$$\lambda_{A-2} = f_2|_A > 0, \quad (11)$$

355
$$\lambda_{A-3} = f_3|_A > 0. \quad (12)$$

356 The stable eigenvalue (λ_{A-1}) is given by the response of the blooming autotroph to increases in its
 357 own biomass ($\frac{\partial f_1}{\partial u_1}$) and is always negative, as autotroph growth rate reduces as nutrient becomes

358 less available. The other eigenvalues are obtained by evaluating the growth functions (f_i) of the
 359 zPFTs at the critical point. These reflect the grazing pressures applied by the predators
 360 (λ_{A-2} and λ_{A-3}). Systems that comply with Kolomogorov's criteria will always have λ_{A-2} and
 361 λ_{A-3} positive (destabilising) at this point. The directions of these eigenvalues will vary according to
 362 the nature of the f_i , but will always point into the interior of, and lie in the plane of, the (u_1, u_2)
 363 plane for λ_{A-2} or the (u_1, u_3) plane for λ_{A-3} .

364

365

366 **Predator-Prey Critical Points (B, C):**

367

368 Every sub-system that complies with Kolmogorov's criteria will have a predator-prey critical point.

369 In the system defined by equation (1) these are defined by $u_1^* \neq 0, u_2^* \neq 0, u_3^* = 0$ for B and

370 $u_1^* \neq 0, u_2^* = 0, u_3^* \neq 0$ for C, and are located where the $f_1 = 0$ isocline intersects the $f_2 = 0$ isocline

371 in the (u_1, u_2) plane and where the $f_1 = 0$ isocline intersects the $f_3 = 0$ isocline in the (u_1, u_3) plane

372 respectively. The eigenvalues of these critical points are given by:

$$373 \quad 2\lambda_{B-1,2} = \frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_2}{\partial u_2} u_2 \pm \sqrt{\left(\frac{\partial f_1}{\partial u_1} u_1 - \frac{\partial f_2}{\partial u_2} u_2\right)^2 + 2 \frac{\partial f_1}{\partial u_2} \frac{\partial f_2}{\partial u_1} u_1 u_2} \Big|_B, \quad (13)$$

374

$$\lambda_{B-3} = f_3 \Big|_B, \quad (14)$$

375 for B, and by:

$$376 \quad 2\lambda_{C-1,3} = \frac{\partial f_1}{\partial u_1} u_1 + \frac{\partial f_3}{\partial u_3} u_3 \pm \sqrt{\left(\frac{\partial f_1}{\partial u_1} u_1 - \frac{\partial f_3}{\partial u_3} u_3\right)^2 + 2 \frac{\partial f_1}{\partial u_3} \frac{\partial f_3}{\partial u_1} u_1 u_3} \Big|_C, \quad (15)$$

377

$$\lambda_{C-2} = f_2 \Big|_C, \quad (16)$$

378 for C. Kolmogorov showed that in almost all cases $\lambda_{B-1,2}$ and $\lambda_{C-1,3}$ will be complex numbers, with

379 positive or negative real parts, indicating that trajectories will either spiral into or away from the

380 critical point. The exceptions to this general case occur if parameter values are varied so that the

381 predator-prey critical point approaches the critical points at the extremes of the prey axis, the origin

382 and the prey-only critical points. These points are both saddles, and as the predator-prey point
 383 closes on them, just prior to colliding with them and undergoing a transcritical bifurcation it must
 384 lose its complex eigenvalues and acquire real eigenvalues of opposite sign, so that at the point of
 385 collision the eigenvalues of both points are identical.

386

387 Spiral curves then lie in the (u_1, u_2) or (u_1, u_3) planes and start or end at B or C. $\lambda_{B-1,2}$ and $\lambda_{C-1,3}$
 388 therefore control the dynamics in the (u_1, u_2) and (u_1, u_3) planes respectively. The dynamics of the
 389 system in the direction orthogonal to these planes is controlled by the eigenvalues λ_{B-3} and λ_{C-2} .
 390 These eigenvalues are of critical importance to PFT modellers as they determine whether a system
 391 will maintain all PFTs extant during simulations. These eigenvalues are associated with
 392 eigenvectors that are orthogonal to the (u_1, u_2) and (u_1, u_3) planes respectively, with magnitudes
 393 given by the f_i of the competing grazer evaluated at the critical point. These eigenvalues are
 394 always real numbers, their direction is known, and analytic expressions for them are easily obtained
 395 from inspection of the model equations. The signs of these eigenvalues determine whether an
 396 interior predator-predator-prey critical point (D), fundamental to the construction of a *bona fide*
 397 PFT model, exists and is stable.

398

399

400 **Predator-Predator-Prey Critical Point (D):**

401

402 As noted above, the system may have a critical point D defined by $u_1^* \neq 0, u_2^* \neq 0, u_3^* \neq 0$ located
 403 where the $f_1 = 0, f_2 = 0$ and $f_3 = 0$ isoclines all intersect in the (u_1, u_2, u_3) volume. In this case
 404 the isoclines are surfaces; typical isocline surfaces are shown in Fig. 1. The existence of this point is
 405 not assured by Kolmogorov's criteria as it is a predator-predator-prey system rather than a predator-
 406 prey system. However, systems that have critical points at B and C will for some parameter sets
 407 have a predator-predator-prey critical point D that lies in the interior of the state space.

408

409 The eigenvalues of the critical point D are generally intricate in analytic form, and difficult to
 410 interpret, as they involve the roots of a cubic equation derived from the community matrix, and
 411 hence it is usually more efficacious to obtain them numerically. Generally, the spiral dynamics
 412 enforced on the (u_1, u_2) and (u_1, u_3) planes by the Kolmogorov criteria are observed throughout the

413 interior of the state space. We therefore expect that the critical point D will have one pair of
 414 complex conjugate eigenvalues that control its spiral behaviour in the $(P, \xi_1 Z_1 + \xi_2 Z_2)$ ‘plane’,
 415 where ξ_1 and ξ_2 are constants defining a ray on the (Z_1, Z_2) face. The third eigenvalue must be a
 416 real number, and its sign will control the outcome of the competition between the two grazers. The
 417 real eigenvalue will therefore either repel trajectories away from D toward the predator-prey critical
 418 points on the faces (if positive) or attract them away from the faces toward the interior predator-
 419 predator-prey critical point D (if negative). This eigenvalue is therefore analogous to the long-term
 420 low-density growth rate for each competing species that is a central tenet of invasion theory in
 421 terrestrial plant communities.

422

423 The global dynamics of the state space must be consistent with the above local information.
 424 Therefore, if both predator-prey boundary critical points have positive real eigenvalues, consistency
 425 of the vector field requires the existence of an interior critical point with negative real eigenvalues.
 426 This will be a stable coexistence point, as the dynamics in the orthogonal direction, determined by
 427 the sign of the real parts of the complex conjugate eigenvalue pair of this point, is irrelevant, as
 428 shown in CN09. The relevant stability properties of the boundary points are the instability due to
 429 positive real eigenvalues pointing to the interior of the state space. Instability in the predator-prey
 430 plane (i.e. whether they have stable spirals or limit cycles in the absence of the other predator) does
 431 not affect coexistence.

432

433 Similar arguments apply for predator-prey boundary critical points that both have negative real
 434 eigenvalues, and for those points that have real eigenvalues of opposite sign. If the critical points on
 435 the faces B and C both have negative real eigenvalues associated with the eigenvectors that are
 436 orthogonal to the faces, the interior critical point D must have positive real eigenvalues, and
 437 consequently not be a coexistence point. In the case where B and C have real eigenvalues of
 438 opposite signs, D cannot exist in the interior of the state space. In this circumstance, the point is
 439 located exterior to the ecologically feasible state space, and it and its eigenvalues do not influence
 440 the dynamics of the system.

441

442

443 **Ubiquity of valid parameter sets**

444 The results of the parameter searches for each of the functional forms are summarised in Table 3
 445 and reveal several interesting properties of the NPZ_1Z_2 system. The first is that including quadratic

446 forms for mortality for both zooplankton and phytoplankton generally increases the number of valid
 447 parameter sets found. The NPZ_1Z_2 system with quadratic mortality for both zooplankton and the
 448 phytoplankton functional types had 83% of randomly selected parameter sets that were valid,
 449 whereas only 61% of parameter sets were valid in the equivalent systems with all linear mortality
 450 terms. The percentage of valid parameter sets increased approximately linearly with the number of
 451 PFTs that had nonlinear mortality, indicating that the inclusion of nonlinear mortality is indeed a
 452 useful tool in building *bona fide* PFT models.

453
 454 The distributions of the competition eigenvalues of the valid parameter sets other than [0000],
 455 [0100], [0011] and [0111] (see below) are shown in Figs 2-4. In these figures, eigenvalue
 456 combinations that result in *bona fide* PFT systems are located in the front quadrant ($\lambda_{B-3} > 0$ and
 457 $\lambda_{C-2} > 0$), pseudo-PFT systems in the rear quadrant ($\lambda_{B-3} < 0$ and $\lambda_{C-2} < 0$), and non-PFT systems
 458 in the left and right quadrants. A characteristic of all these distributions is that they are all
 459 asymmetric, with the asymmetry determined by which zPFT has nonlinear mortality and/or whether
 460 omnivory of Z_2 on Z_1 is allowed. Table 3 indicates that pseudo-PFT parameter sets, for which the
 461 initial conditions determine which zPFT will ultimately survive, are the least common type of PFT
 462 system for NPZ_1Z_2 systems. No pseudo-PFT parameter sets were observed for systems without
 463 zooplankton omnivory, or for systems for which the omnivore had nonlinear mortality. Pseudo-PFT
 464 systems were observed only for less than 6% of systems that had an omnivore with linear mortality.

465

466

467 **Classes of *bona fide* PFT parameter sets**

468

469 Our results reveal that the *bona fide* NPZ_1Z_2 systems may be classified into several subtypes
 470 characterised by the functional forms and/or trophic structures of the models. The analysis showed
 471 that the sixteen model formulations could be classified according to the probability of finding
 472 parameter sets that resulted in *bona fide* dynamics:

- 473 • always *bona fide* PFT systems: no omnivory and both zPFT have nonlinear mortality
 474 ([0011] and [0111])
- 475 • common (high probability) *bona fide* PFT systems: no omnivory and one zPFT has linear
 476 mortality and the other nonlinear mortality ([0001], [0010], [0101] and [0110])

- 477 • intermediate (moderate probability) *bona fide* PFT systems: omnivory and the top predator
 478 has linear mortality ([1000], [1010], [1100] and [1110])
- 479 • rare (low probability) *bona fide* PFT systems: omnivory and the top predator has nonlinear
 480 mortality ([1001], [1011], [1101] and [1111])
- 481 • never *bona fide* PFT systems: no omnivory and both zPFT have linear mortality ([0000] and
 482 [0100])

483 This categorisation, based on probabilities of finding *bona fide* parameter sets, will be used in the
 484 figures and discussion of the properties of the models as other similarities are also captured by this
 485 classification scheme.

486

487 Systems that always or never have co-existing zPFTs ([0000], [0100], [0011] and [0111]) have very
 488 uninteresting properties in the context of this paper, with their eigenvalues all symmetrically
 489 grouped near zero and uniform parameter distributions, so we somewhat pragmatically group these
 490 together as uninteresting systems and ignore them in the following analysis. We now consider only
 491 the properties of the other three types of system.

492

493

494 **Properties of common *bona fide* PFT systems**

495

496 Common *bona fide* PFT systems have zooplankton that are not omnivorous and have one zPFT
 497 with linear mortality and one zPFT with nonlinear mortality. The valid parameters for these systems
 498 have asymmetric distributions of the competition eigenvalues λ_{B-3} and λ_{C-2} (Fig 2) with the
 499 asymmetry being determined by which of the zPFT has nonlinear mortality. The zPFT with
 500 nonlinear mortality has the competition eigenvalue of its predator-prey critical point negative,
 501 indicating that it will send the competing zPFT extinct. Therefore, in the approximately 80% of
 502 these valid parameter sets that produce non-PFT systems, the zPFT with nonlinear mortality will
 503 dominate and the zPFT with linear mortality will become extinct. However, approximately 20% of
 504 these parameter sets will produce *bona fide* PFT systems, in which the other attributes of the zPFT
 505 with linear mortality compensate for the competitive advantage endowed upon the competing zPFT
 506 by nonlinear mortality and allow both PFTs to coexist.

507

508 The attributes of the competing zooplankton that allow coexistence in common *bona fide* PFT
 509 systems, as described by the parameter distributions, are shown in Fig 5. In order to coexist the

510 zPFT with nonlinear mortality (Z_{NL}) must exert very light grazing pressure on the pPFT (ϕ_{NL}
 511 small) and be an inefficient converter of food to biomass (ψ_{NL} large), while the zPFT with linear
 512 mortality (Z_L) exerts moderate to heavy grazing pressure (ϕ_L moderate to large) and efficiently
 513 converts food to biomass (ψ_L small). Similarly, Z_L must have very low mortality coefficient (σ_L)
 514 while Z_{NL} has a moderate to large coefficient (σ_{NL}). The ‘half-saturation’ constants (ε_1 and ε_2)
 515 have little influence on the coexistence of the zPFTs, suggesting that stable equilibria or stable limit
 516 cycles are equally likely.

517

518 **Properties of intermediate *bona fide* PFT systems**

519

520 Intermediate *bona fide* PFT systems have an omnivorous zPFT (Z_2) that has linear mortality. The
 521 valid parameters for these systems also have asymmetric distributions of the competition
 522 eigenvalues λ_{B-3} and λ_{C-2} (Fig 3) with the asymmetry being dominated by the omnivore. These
 523 systems have the most potential behaviours, with Table 3 revealing that 7-10% of valid parameter
 524 sets produce *bona fide* PFT systems, 1-6% produce pseudo-PFT systems and 85-90% produce non-
 525 PFT systems. Of the non-PFT systems, Fig 3 reveals that the Z_2 will send Z_1 extinct in most cases,
 526 but there are some parameter sets that allow Z_1 to send Z_2 extinct.

527

528 Comparison of the parameter distributions of these *bona fide* PFT systems (Fig 6) with Fig 5
 529 reveals that the zooplankton attributes that allow coexistence in these systems are quite different
 530 from common *bona fide* PFT systems. The likelihood of coexistence in these systems is insensitive
 531 to the rate of Z_2 grazing on phytoplankton (ϕ_2), but is increased if Z_1 grazes heavily on the pPFT
 532 (ϕ_1 moderate to large). Low to moderate coefficients for Z_1 respiration (ψ_1) again maximise the
 533 potential for coexistence, which is more likely if Z_2 inefficiently converts food to biomass, but in
 534 contrast to common systems, there is an optimal maximum value for Z_2 respiration of about
 535 $\psi_2 = 0.9$.

536

537 The distribution of parameter values for the Z_2 mortality coefficient (σ_2) also has an optimum
 538 value in these systems, but is relatively insensitive to the Z_1 mortality coefficient (σ_1). In this case,

539 $\sigma_2 \approx 0.25$ appears to provide the optimum likelihood of coexistence (the actual value of σ_2 used in
 540 model simulations will depend on the values of the pPFT growth parameters, as we have used non-
 541 dimensional parameters in our analysis). Again, the ‘half-saturation’ constants for zPFT grazing on
 542 the pPFT (ε_1 and ε_2) have little influence on the coexistence of the zPFTs.

543

544 **Properties of rare *bona fide* PFT systems**

545

546 Rare *bona fide* PFT systems have an omnivorous zPFT (Z_2) that has nonlinear mortality. The valid
 547 parameters for these systems have strongly asymmetric distributions of the competition eigenvalues
 548 λ_{B-3} and λ_{C-2} (Fig 4) with the system either supporting both zPFTs (less than 5% of valid
 549 parameter sets) or in 95% of cases Z_2 drives Z_1 to extinction. No parameter sets were found such
 550 that these systems exhibited pseudo-PFT dynamics where the initial conditions determined which
 551 zPFT went extinct.

552

553 The distributions of the parameters of these systems (Fig 7) reveal similar heuristics to those of
 554 common *bona fide* PFT systems, with very similar distributions of grazing pressures (φ_1, φ_2) and
 555 assimilation efficiencies (ψ_1, ψ_2). These parameter distributions indicate that the omnivorous zPFT
 556 needs to be a ‘lazy’ and inefficient predator for the other zPFT to survive. Similarly, coexistence is
 557 more likely if the prey zPFT is a voracious grazer and converts food to biomass efficiently. The
 558 distribution of mortality parameters is more similar to that of intermediate *bona fide* PFT systems,
 559 in that coexistence is essentially determined by the omnivore’s mortality coefficient and is
 560 insensitive to the prey zPFT’s mortality rate. This relationship is different from that observed for
 561 intermediate systems, as the likelihood of coexistence appears to increase linearly with the
 562 omnivore’s mortality coefficient.

563

564

565 **DISCUSSION**

566

567 The results of the analysis of the NPZ_1Z_2 system in this paper are broadly consistent with the
 568 results of the analysis of the NP_1P_2Z system discussed in CN09 in that:

- 569 • *Bona fide* PFT parameter sets are rare in parameter space: less than 10% of valid parameter
 570 sets produced *bona fide* dynamics in omnivorous systems; if omnivory was prohibited,
 571 approximately 20% of valid parameter sets produced *bona fide* dynamics. This is compared
 572 to 0.6% for the NP_1P_2Z system analysed in CN09.
- 573 • *Bona fide* PFT parameter sets are distributed throughout parameter space for many systems.
 574 Generally, *bona fide* parameter sets are more common in some regions of parameter space
 575 than others, but depending on the process formulations (f_i) used, some regions of parameter
 576 space are highly unlikely to produce *bona fide* PFT systems.
- 577 • PFT models require finely tuned parameter sets in order to keep all functional types extant.

578 We reiterate that in drawing these conclusions we have not considered systems that always have an
 579 internal critical point ([0011] and [0111]) and those that never have an internal critical point ([0000]
 580 and [0100]). These systems all have uniform parameter distributions that do not contribute to our
 581 analysis.

582

583 The analyses of CN09 and this paper have revealed that NP_1P_2Z and NPZ_1Z_2 systems have quite
 584 different likelihoods of parameter sets that result in pseudo-PFT systems, where the winner of
 585 competition between functional types is determined by the initial conditions. CN09 found that about
 586 7% of valid parameter sets resulted in pseudo-PFT dynamics, whereas this analysis found many
 587 systems for which these dynamics appear not possible. Of the 16 model formulations examined,
 588 pseudo-PFT dynamics were only found in four systems; of these systems, less than 6% of valid
 589 parameter sets produced pseudo-PFT systems. These systems all included omnivory where the
 590 omnivorous zPFT had linear mortality.

591

592 The additional insights that analysis of the NPZ_1Z_2 systems provides over the analysis of the
 593 NP_1P_2Z system of CN09 are that omnivory and mortality are important contributors to the
 594 likelihood of finding *bona fide* PFT parameter sets where competing zPFTs can coexist indefinitely.
 595 This is consistent with other studies that have observed the importance of these factors for the
 596 dynamics and stability of food web models (Steele and Henderson 1992, Edwards and Yool 2000,
 597 Emmerson and Yearsley 2004).

598

599

600 **Symmetry**

601

602 The analysis of the NPZ_1Z_2 model in this paper has noted similarities with the analysis of the
 603 NP_1P_2Z model reported in CN09. However, the models differ quite fundamentally in their
 604 symmetry properties. The NP_1P_2Z model analysed in CN09 had a symmetric trophic topology, and
 605 the frequency distributions of the competition eigenvalues (Fig 7 in CN09) and the competition
 606 parameters of the *bona fide* parameter sets (Fig 9 in CN09) were also symmetric. While rare, the
 607 *bona fide* parameters were distributed ubiquitously throughout the parameter space, with no regions
 608 of the space having zero density of *bona fide* parameters.

609

610 The analysis of the NPZ_1Z_2 system in this paper suggests that, in contrast to systems with multiple
 611 autotrophs, symmetric trophic topologies are rare in systems with multiple grazers that exist in
 612 constant, homogeneous environments. The purely symmetric systems ([0000], [0011], [0100] and
 613 [0111]) could never have, or always had, stable interior critical points for all valid parameter sets.
 614 The asymmetry of *bona fide* NPZ_1Z_2 systems is evident throughout the distributions of the
 615 eigenvalues (Figs 2-4) and most of the competition parameters (Figs 5-7). In systems that do not
 616 have omnivory, the asymmetry is driven by the form of the zPFT mortality terms, whereas in
 617 systems that include omnivory the asymmetry is driven by the direction of the omnivory, but its
 618 effects may be modified by the form of the zPFT mortality terms. Further, in contrast to the
 619 competition parameter distributions of the NP_1P_2Z model reported in CN09 there are substantial
 620 regions of the competition parameter space where the density of *bona fide* parameter sets falls to
 621 zero. This is particularly evident for the mortality parameters (σ_1 and σ_2) and the assimilation
 622 efficiency parameters (ψ_1 and ψ_2) in systems without omnivory (Fig 5) and in the systems with
 623 omnivory in which the top predator has nonlinear mortality (Fig 7). The distributions are less
 624 strongly asymmetric in systems that have omnivory in which the prey zPFT has nonlinear mortality
 625 and the predator zPFT has linear mortality (Fig 6). The parameter distributions of these systems
 626 reveal optimal parameter combinations driven by trade-offs between the competitive advantages
 627 provided to the prey zPFT by nonlinear mortality and those provided to the predator zPFT by
 628 omnivory.

629

630 **Omnivory and mortality**

631

632 While once Gause's (1934) 'competitive exclusion principle' was considered to be the norm, recent
 633 workers have suggested that attributes such as density-dependent mortality can prevent competitive
 634 exclusion (Ruan et al. 2007). The form that such density-dependent mortality should take is,
 635 however, a matter of debate (Edwards and Brindley 1999, Edwards and Yool 2000, Edwards and
 636 Bees 2001, Mitra 2009). Ruan et al (2007) considered competing predators without omnivory
 637 where the grazers had Holling Type II grazing interactions (equivalent in our model to $\phi = 0$ and
 638 $\varepsilon_1, \varepsilon_2 \neq 0$) and concluded that the use of a density-dependant (in fact quadratic) mortality term for
 639 one competitor 'not only ensures the survival of itself, but also guarantees the existence of the other
 640 competitor, which would otherwise be out-competed'. Ruan et al. (2007) considered only the cases
 641 for which the internal predator-predator-prey critical point existed, and determined conditions for its
 642 stability. In the parlance of this paper, they examined the influence of nonlinear mortality on the
 643 stability of the interior critical point and concluded that systems with nonlinear mortality could not
 644 have pseudo-PFT parameter sets. Our analysis (of models with quite different functional forms)
 645 agrees with their conclusion; when one or other zPFT in our NPZ_1Z_2 system without omnivory had
 646 nonlinear mortality we did not find any parameter sets that resulted in pseudo-PFT systems,
 647 suggesting that this may be a quite general property of PFT systems.

648
 649 The role of omnivory in maintaining competing species extant in food web models has also
 650 received recent attention, with Vandermeer (2006) concluding that omnivory may be stabilizing or
 651 destabilising (where they use 'stable' to mean the persistence of the competing species), depending
 652 on the structure of the food web. Our results are consistent with Vandemeer's conclusions; if
 653 omnivory is added to model structures in which one or both zPFTs have nonlinear mortality
 654 ([0001], [0010], [0011], [0101], [0110] or [0111]), the addition of omnivory is 'destabilising'. In
 655 these cases, the addition of omnivory reduces the likelihood of finding *bona fide* parameter sets
 656 from around 20% (or 100% in the cases of [0011] and [0111]) to 3-10%. Conversely, the addition
 657 of omnivory to systems that are unstable, in that competitors cannot coexist ([0000] and [0100]),
 658 'stabilises' the systems, with the likelihood of finding *bona fide* parameter sets increasing from zero
 659 to around 7%.

660

661 **Interaction strengths**

662

663 Our *bona fide* systems reveal a skewed distribution of interaction strengths (parameter values and
 664 fluxes) toward weaker interactions, and we note that this appears a common property of stable high-

665 dimension ecosystem models. This property was observed by McCann et al (1998) in a study of six
666 food-web models, and appears common to stable food webs with omnivores in particular (Namba et
667 al. 2008). For example Emmerson and Yearsley (2004) examined randomly generated Lotka-
668 Volterra systems and concluded that species were more likely to coexist in omnivorous food webs if
669 the omnivorous interactions were weak. Similarly, McCann and Hastings (1997) noted that
670 relatively strong omnivory could cause a three-species food web model to lose its interior critical
671 point.

672
673 Weak interactions, however, generally result in food webs that are slow to recover from
674 perturbation (Emmerson and Yearsley 2004), and that may be less resistant to species loss (Borvall
675 et al. 2000). This presents what may be an interesting conundrum, as ecological parameter spaces
676 are poorly constrained, and modellers generally have little option but to use parameter sets that
677 ‘best’ reproduce observed data. The paucity of *bona fide* parameter sets in the regions of parameter
678 space that produce high-interaction strength models, and the significant computational demands
679 associated with parameterising even quite modestly complex PFT models, suggest that such ‘best-
680 fit’ approaches will be biased toward systems with low interaction strengths. While these regions of
681 parameter space may produce *bona fide* PFT systems that do a reasonable job of reproducing
682 observed data, there is some reason to question whether these regions are representative of the
683 ecosystems that exist in nature.

684
685 Unfortunately, unlike modellers of physical systems, ecosystem modellers as yet have little
686 overarching theory to guide them in parameterising models (Hood et al. 2007). The consideration of
687 theories that shape ecosystem adaptation was perhaps initiated in the contemporary era by Lotka
688 (1922), who suggested that natural selection would operate, within the constraints of the
689 environment and the potential of the organisms, to maximise the energy flux through an ecosystem.
690 Odum (1983) elaborated this concept into the ‘maximum power principle’ and similarly suggested
691 that ecosystems would maximise the flow of useful energy, while Schneider (1988) proposed a
692 theory of maximum entropy production. Recently, Kleidon (2004, 2009) has extended the concept
693 of maximum entropy production to the Earth system.

694
695 Cropp and Gabric (2002) synthesised these, and related concepts of maximum exergy (Jorgensen
696 1992) and maximum ascendancy (Ulanowicz 1980), with ecological considerations such as
697 maximum production per unit biomass (Lotka 1922, Odum and Pinkerton 1955) and resilience
698 (DeAngelis 1992) into ecologically-defined ‘thermodynamic imperatives’ and simulated the effect

699 of these imperatives on the evolution of the biotic constituents of a simple ecosystem model. They
700 discovered that the outcomes produced by these imperatives were consistent, and that the parameter
701 set that maximised the resilience of the system also optimised the other imperatives. Most
702 importantly in the context of this paper, these parameter sets also maximised the interaction
703 strengths. Laws (2003) has since demonstrated the efficacy of using this maximum resilience
704 approach for fitting ecosystem models to data, suggesting that real ecosystems may have parameter
705 sets that result in resilient systems with large interaction strengths.

706

707 Our results suggest that unsophisticated searches of parameter space looking merely for parameter
708 sets that allow the models to reproduce observed data with some ‘acceptable’ level of veracity may
709 not be the most useful approach. Such searches are more likely to be successful in regions of
710 parameter space that result in PFT systems with low interaction strengths because *bona fide*
711 parameter sets are more abundant there. Conversely, parameter sets that generate high interaction
712 strengths are sparse in the parameter space, but satisfy broader theoretical concepts of the properties
713 of ecosystems. Parameterisation approaches that simultaneously maximise interaction strengths and
714 minimise the discrepancy between observations and model predictions are likely to produce better
715 models than simple approaches that seek only to mimic data. The more sophisticated approach is
716 likely to be most effective in high latitude regions of the ocean that function in accordance with
717 Sverdrup’s (1953) criteria for bloom development. In these regions, ecosystem dynamics closely
718 track physical forcings such as irradiance and temperature, suggesting that the ecosystems are
719 highly resilient (Gabric et al. 2003).

720

721

722 **CONCLUSIONS**

723

724 The analysis of this predator-predator-prey (NPZ_1Z_2) system again emphasises the great advantage
725 of Kolmogorov systems that analytic expressions for the eigenvalues that control the ability of a
726 PFT to invade and/or coexist in an ecosystem may be obtained directly from inspection of the
727 governing equations. We recall that these eigenvalues are explicit representations of the long-term
728 low-density growth rates that are central to invasion theory developed from terrestrial plant
729 communities.

730

731 This work also provides some useful heuristics to guide biogeochemical modellers in the
 732 construction and parameterisation of PFT models. These heuristics extend the heuristics for the
 733 predator-prey-prey (NP_1P_2Z) model reported in CN09 (Cropp and Norbury 2009a) and include:

- 734 • In contrast to symmetric prey-prey-predator systems, that contribute insights in to the
 735 properties of competing prey in homogenous, stable environments, symmetric predator-
 736 predator-prey models can apparently contribute little.
- 737 • Consequently, distributions of competition parameters that lead to *bona fide* dynamics in
 738 predator-predator-prey models are strongly asymmetric. Unlike predator-prey-prey systems,
 739 there are likely to be regions of parameter space where the likelihood of finding *bona fide*
 740 parameter sets falls to zero.
- 741 • The use of nonlinear mortality terms for predators makes them ‘super-competitors’ that are
 742 very resistant to extinction. Systems with multiple predators that include omnivory are
 743 therefore more likely to have *bona fide* dynamics if the top predator has linear mortality and
 744 their competitor/prey has nonlinear mortality.
- 745 • Distributions of interaction strengths of *bone fide* PFT systems are skewed towards weak
 746 interactions, suggesting that calibration exercises to find parameter sets that mimic
 747 observations are more likely to produce models with this attribute. However, theoretical
 748 considerations suggest that modellers should search for such parameter sets in the regions of
 749 parameter space where interactions are strong, but *bone fide* parameter sets are rare.

750 We also note that whereas the consideration of competition in terrestrial plant communities has
 751 resulted in an emphasis on the role of spatial and temporal variation in ensuring coexistence, our
 752 analysis shows that coexistence in competitive plankton communities is possible in constant,
 753 homogeneous environments.

754
 755 It would appear from a comment made by a reviewer of CN09 that the initial response of PFT
 756 modellers to the difficulties of parameterising PFT models, that we have explicated in CN09 and
 757 again in this paper, has been to include computational ‘fixes’ in their code that prevent PFTs from
 758 going extinct in simulations. This increases the probability of finding useful parameter sets, making
 759 such models much easier to parameterise. However, we suggest that such fixes inevitably lead to
 760 flawed models, that in particular are unable to predict changes in community structure and species
 761 extinctions in the plankton that may already be happening (Montes-Hugo et al. 2009).

762

763 We hope that the heuristics we have presented here, in conjunction with those presented in CN09,
 764 will prove useful in the construction and parameterisation of particularly those plankton
 765 biogeochemical models currently being developed to model the contribution of ocean biota to
 766 climate, and alleviate the temptation of such ‘fixes’. In particular, we note that the use of eigenvalue
 767 properties to search a model’s parameter space can provide significant benefits in terms of
 768 computational load, and reductions of CPU time of six orders of magnitude are not unrealistic.

769
 770 Finally, we observe that while the heuristics presented in this paper may be combined to guide the
 771 development of higher-dimension PFT models to ensure *bona fide* dynamics, more behaviours are
 772 possible in the higher-dimension models. Our analyses therefore need to be extended to incorporate
 773 these additional potential behaviours, and we hope to present these analyses in forthcoming work.

774

775

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777

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779

780

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925 **FIGURE LEGENDS**

926

927 Figure 1. Generic diagram of one autotroph and two grazer isoclines showing intersection of the
 928 grazer isoclines ($f_2 = 0$ and $f_3 = 0$) with the autotroph isocline ($f_1 = 0$) to give an internal critical
 929 point (D). The competition eigenvalues (equivalent to the competing species long-term low-density
 930 growth rates) that are crucial to coexistence are shown as the black double-ended arrows at critical
 931 points B and C.

932

933 Figure 2. Frequency distributions of the two competition eigenvalues λ_{B-3} and λ_{C-2} for common
 934 systems. Recall that we use codes such as [0101] to denote the values of $[\phi, \alpha, \gamma, \delta]$. Eigenvalue
 935 combinations that result in *bona fide* PFT systems are located in the front quadrant ($\lambda_{B-3} > 0$ and
 936 $\lambda_{C-2} > 0$), pseudo-PFT systems in the rear quadrant ($\lambda_{B-3} < 0$ and $\lambda_{C-2} < 0$), and non-PFT systems
 937 in the left and right quadrants.

938

939 Figure 3. Frequency distributions of the two competition eigenvalues λ_{B-3} and λ_{C-2} for
 940 intermediate systems. Details as for Fig 2.

941

942 Figure 4. Frequency distributions of the two competition eigenvalues λ_{B-3} and λ_{C-2} for rare
 943 systems. Details as for Fig 2.

944

945 Figure 5. Typical frequency distributions of the four competition zPFT parameter pairs for common
 946 systems. The parameter pairs are grazing (φ_1, φ_2) (a), half-saturation ($\varepsilon_1, \varepsilon_2$) (b), mortality (σ_1, σ_2)
 947 (c) and assimilation efficiency (ψ_1, ψ_2) (d). Distributions shown are for system [0001]; the other
 948 common systems ([0010], [0101] and [0110]) have the same distributions.

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950 Figure 6. Typical frequency distributions of the four competition zPFT parameter pairs for
 951 intermediate systems. Panels as for Fig 5. Distributions shown are for system [1000]; the other
 952 intermediate systems ([1010], [1100] and [1110]) have the same distributions.

953

954 Figure 7. Typical frequency distributions of the four competition zPFT parameter pairs for rare
 955 systems. Panels as for Fig 5. Distributions shown are for system [1001]; the other rare systems
 956 ([1011], [1101] and [1111]) have the same distributions.

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959 **TABLES**

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962 **Table 1: Parameter bounds used to constrain the parameter searches for the NPZ_1Z_2 model. These**
 963 **values are identical to those used in CN09 and have been non-dimensionalised from measured values.**

964

PAR	PROCESS	VALUE
μ	Maximum rate of N uptake by P_1	0.25 – 1.70
κ	Half-saturation constant for P_1 uptake of N	0.00 – 1.00
$\varphi_1, \varphi_2, \tilde{\varphi}$	Z_1 or Z_2 grazing rate (per ind) on Z_1 and/or P	0.75 – 9.00
$\varepsilon_1, \varepsilon_1, \tilde{\varepsilon}$	Half-saturation constant for Z_1 or Z_2 uptake of Z_1 and/or P	0.00 – 2.00
$\sigma, \sigma_1, \sigma_2$	P, Z_1 or Z_2 specific mortality rate	0.00 – 0.50
α, γ, δ	P, Z_1 or Z_2 mortality exponents	0 or 1
$\psi_1, \psi_2, \tilde{\psi}$	Proportion of P or Z_1 uptake excreted by Z_1 or Z_2	0.01 – 0.99

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Table 2: Criteria for classification of parameter sets for the NPZ_1Z_2 system.

CRITICAL PT	CRITERION	METRIC
<u>Validity</u>		
A	$0 < P_A^* < 1$	$0 < \frac{\mu - \sigma(1 + \kappa)}{\mu - \sigma} < 1, \quad (\alpha = 0)$
		$0 < \frac{\mu + \sigma(1 + \kappa) \pm \sqrt{[\mu + \sigma(1 + \kappa)]^2 - 4\mu\sigma}}{2\sigma} < 1, \quad (\alpha = 1)$
B ¹	$0 < P_B^* < 1$	$0 < \frac{\sigma_1 Z_{1B}^{*\gamma}}{\varphi_1(1 - \psi_1) - \varepsilon_1 \sigma_1 Z_{1B}^{*\gamma}} < 1$
	$0 < Z_{1B}^* < 1$	$0 < \left(\frac{1 + \varepsilon_1 P_B^*}{\varphi_1(N_B^* + \kappa)} \right) \left[\sigma_1 (N_B^* + \kappa) P_{1B}^{*\alpha} - \mu N_B^* \right] < 1$
C ²	$0 < P_C^* < 1$	$0 < \frac{\sigma_2 Z_{2C}^{*\gamma}}{\varphi_2(1 - \psi_2) - \varepsilon_2 \sigma_2 Z_{2C}^{*\gamma}} < 1$
	$0 < Z_{2C}^* < 1$	$0 < \left(\frac{1 + \varepsilon_2 P_C^*}{\varphi_2(N_C^* + \kappa)} \right) \left[\sigma_2 (N_C^* + \kappa) P_{2C}^{*\alpha} - \mu N_C^* \right] < 1$
<u>Bona fide</u>		
B	$\lambda_{B-3} = f_{Z_2} \Big _B > 0$	$\frac{\varphi_2(1 - \psi_2)P_B^*}{1 + \varepsilon_2 P_B^*} + \frac{\phi(1 - \psi)Z_{1B}^*}{1 + \varepsilon Z_{1B}^*} - \sigma_2 Z_{2B}^{*\delta} > 0$
C	$\lambda_{C-2} = f_{Z_1} \Big _C > 0$	$\frac{\varphi_1(1 - \psi_1)P_C^*}{1 + \varepsilon_1 P_C^*} - \frac{\phi Z_{2C}^*}{1 + \varepsilon Z_{1C}^*} - \sigma_1 Z_{1C}^{*\gamma} > 0$

971 ¹ N_B^* is given by equation (29) or (30)

972 ² N_C^* is given by equation (33) or (34)

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Table 3: Results of searches of the parameter space for the NPZ_1Z_2 model. One million randomly selected parameter sets were evaluated for validity and for the existence and stability of an interior point for each model formulation.

PARAMETER				VALID		<i>Bona fide</i> PFT		Pseudo-PFT		Non-PFT	
$\tilde{\phi}$	α	γ	δ	No	%	No	%	No	%	No	%
0	0	0	0	609,584	61	0	0	0	0	609,584	100
0	0	0	1	664,287	66	124,835	18.8	0	0	539,452	81.2
0	0	1	0	663,559	66	124,145	18.7	0	0	539,414	81.3
0	0	1	1	768,969	77	768,969	100	0	0	0	0
0	1	0	0	704,617	70	0	0	0	0	704,617	100
0	1	0	1	740,382	74	169,296	22.9	0	0	571,086	77.1
0	1	1	0	739,888	74	169,798	22.9	0	0	570,090	77.1
0	1	1	1	830,548	83	830,548	100	0	0	0	0
$\neq 0$	0	0	0	609,689	61	42,829	7.0	9,915	1.6	556,945	91.4
$\neq 0$	0	0	1	663,204	66	21,917	3.3	0	0	641,287	96.7
$\neq 0$	0	1	0	663,801	66	58,727	8.8	39,329	5.9	565,745	85.3
$\neq 0$	0	1	1	768,747	77	37,152	4.8	0	0	731,595	95.2
$\neq 0$	1	0	0	705,172	71	53,088	7.5	8,802	1.2	643,283	91.3
$\neq 0$	1	0	1	740,108	74	27,505	3.7	0	0	712,603	96.3
$\neq 0$	1	1	0	740,489	74	70,720	9.5	30,638	4.1	639,131	86.4
$\neq 0$	1	1	1	830,522	83	40,467	4.9	0	0	790,055	95

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NOTE: As the value of $\tilde{\phi}$ has no effect on the validity of each parameter set, comparison of equivalent functional forms for $\tilde{\phi} = 0$ and $\tilde{\phi} \neq 0$ provides an indication of the variation in the results associated with the random selection of the parameter sets. This is of the order of less than 0.1%. However, we also note that the percentages of the different solutions for each model will change if the parameter space is changed; the search results should therefore be considered indicative of the types of properties we can expect from generic formulations. Examination of different specific formulations would also change the percentages.

988

989 **APPENDIX**

990

991 We describe the locations and eigenvalues of the critical points of the NPZ_1Z_2 model with linear
 992 phytoplankton mortality ($\alpha = 0$) and quadratic phytoplankton mortality ($\alpha = 1$).

993

994 **Origin Critical Point (O):**

995

996 The critical point at the origin is defined by $P_O^* = Z_{1O}^* = Z_{2O}^* = 0$, $N_O^* = 1$ and has the eigenvalues:

$$997 \quad \lambda_{O-1} = f_P \Big|_O = \frac{\mu}{1 + \kappa} - \sigma \quad (17)$$

$$998 \quad \lambda_{O-2} = f_{Z_1} \Big|_O = -\sigma_1 Z_{1O}^\gamma. \quad (18)$$

$$999 \quad \lambda_{O-3} = f_{Z_2} \Big|_O = -\sigma_2 Z_{2O}^\delta. \quad (19)$$

1000 Note that when $\gamma \neq 0$ and $\delta \neq 0$, $\lambda_{O-2} = 0$ and $\lambda_{O-3} = 0$. This indicates that higher-order terms of
 1001 the system must be considered to elucidate these eigenvalues. However, consideration of these
 1002 terms will produce negative values for λ_{O-2} and λ_{O-3} .

1003

1004 **Prey-only Critical Point (A):**

1005

1006 The prey-only critical point is defined by $Z_{1A}^* = Z_{2A}^* = 0$ and for $\alpha = 0$ is located at:

$$1007 \quad P_A^* = \frac{\mu - \sigma(1 + \kappa)}{\mu - \sigma}, \quad (20)$$

$$1008 \quad N_A^* = \frac{\sigma\kappa}{\mu - \sigma}. \quad (21)$$

1009 For $\alpha = 1$ the point is located at:

1010
$$P_A^* = \frac{\mu + \sigma(1 + \kappa) \pm \sqrt{[\mu + \sigma(1 + \kappa)]^2 - 4\mu\sigma}}{2\sigma}, \quad (22)$$

1011
$$N_A^* = 1 - P_A^*. \quad (23)$$

1012 This point has the eigenvalues:

1013
$$\lambda_{A-1} = \frac{\partial f_1}{\partial u_1} u_1 \Big|_A = -\frac{\mu\kappa}{(N_A^* + \kappa)^2} - \alpha\sigma, \quad (24)$$

1014
$$\lambda_{A-2} = f_{Z_1} \Big|_A = \frac{\varphi_1(1 - \psi_1)P_A^*}{1 + \varepsilon_1 P_A^*} - \sigma_1 Z_{1A}^\gamma, \quad (25)$$

1015
$$\lambda_{A-3} = f_{Z_2} \Big|_A = \frac{\varphi_2(1 - \psi_2)P_A^*}{1 + \varepsilon_2 P_A^*} - \sigma_2 Z_{2A}^\delta. \quad (26)$$

1016 Note that $\lambda_{A-1} < 0$ and $\lambda_{A-2}, \lambda_{A-3} > 0$ for nonlinear mortality ($\gamma, \delta \neq 0$) and will be smaller in
 1017 magnitude for linear mortality, but not negative if the parameter set complies with Kolmogorov's
 1018 criteria.

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1021 **Predator-Prey Critical Points (B, C):**

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1023 The predator-prey critical point on the (P, Z_1) face is given by $Z_{2B}^* = 0$ and:

1024
$$Z_{1B}^* = \left(\frac{1 + \varepsilon_1 P_B^*}{\varphi_1 (N_B^* + \kappa)} \right) \left[\sigma_1 (N_B^* + \kappa) P_{1B}^{*\alpha} - \mu N_B^* \right], \quad (27)$$

1025
$$P_B^* = \frac{\sigma_1 Z_{1B}^{*\gamma}}{\varphi_1 (1 - \psi_1) - \varepsilon_1 \sigma_1 Z_{1B}^{*\gamma}}. \quad (28)$$

1026 Then for $\gamma = 0$

1027
$$2\varphi_1 N_B^* = \left[(1 + \varepsilon_1 P_B^*) (\sigma_1 P_B^{*\alpha} - \mu) + \varphi_1 (P_B^* + \kappa - 1) \right] \pm$$

$$\sqrt{\left[(1 + \varepsilon_1 P_B^*) (\sigma_1 P_B^{*\alpha} - \mu) + \varphi_1 (P_B^* + \kappa - 1) \right]^2 - 4\kappa \left[\sigma_1 (1 + \varepsilon_1 P_B^*) P_B^{*\alpha} - \varphi_1 (P_B^* - 1) \right]}, \quad (29)$$

1028 and for $\gamma = 1$:

1029
$$N_B^* = 1 - P_B^{*\alpha} - Z_{1B}^*, \quad (30)$$

1030 and we obtain the solution for the critical point with quadratic zooplankton mortality numerically.

1031

1032 Similarly, the predator-prey critical point on the (P, Z_2) face is given by $Z_{1C}^* = 0$ and:

1033
$$Z_{2C}^* = \left(\frac{1 + \varepsilon_2 P_C^*}{\varphi_2 (N_C^* + \kappa)} \right) \left[\sigma_2 (N_C^* + \kappa) P_{2C}^{*\alpha} - \mu N_C^* \right], \quad (31)$$

1034
$$P_C^* = \frac{\sigma_2 Z_{2C}^{*\gamma}}{\varphi_2 (1 - \psi_2) - \varepsilon_2 \sigma_2 Z_{2C}^{*\gamma}}. \quad (32)$$

1035 Then for $\gamma = 0$

1036
$$2\varphi_2 N_C^* = \left[(1 + \varepsilon_2 P_C^*) (\sigma_2 P_C^{*\alpha} - \mu) + \varphi_2 (P_C^* + \kappa - 1) \right] \pm$$

$$\sqrt{\left[(1 + \varepsilon_2 P_C^*) (\sigma_2 P_C^{*\alpha} - \mu) + \varphi_2 (P_C^* + \kappa - 1) \right]^2 - 4\kappa \left[\sigma_2 (1 + \varepsilon_2 P_C^*) P_C^{*\alpha} - \varphi_2 (P_C^* - 1) \right]}, \quad (33)$$

1037 and for $\gamma = 1$:

1038
$$N_C^* = 1 - P_C^* - Z_{2C}^*, \quad (34)$$

1039 and we obtain the solution for the critical point with quadratic zooplankton mortality numerically.

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1041

1042 **Predator-Predator-Prey Critical Point (D):**

1043

1044 The predator-predator-prey critical point is defined by $N_D^*, P_D^*, Z_{1D}^*, Z_{2D}^* \neq 0$. The following
 1045 relationships are solved iteratively to obtain the location of the critical point. For $\gamma = 0$, $f_2 = 0$ and
 1046 $f_3 = 0$ provide relationships for P_D^* that must be reconciled; $f_2 = 0$ gives:

$$1047 \quad P_D^* = \frac{\phi Z_{2D}^* + \sigma_1 (1 + \varepsilon Z_{1D}^*)}{(1 + \varepsilon Z_{1D}^*) [\varphi_1 (1 - \psi_1) - \varepsilon_1 \sigma_1] - \varepsilon_1 \phi Z_{2D}^*}, \quad (35)$$

1048 and $f_3 = 0$ gives:

$$1049 \quad P_D^* = \frac{\sigma_2 (1 + \varepsilon Z_{1D}^*) - \phi (1 - \psi) Z_{1D}^*}{(1 + \varepsilon Z_{1D}^*) [\varphi_2 (1 - \psi_2) - \varepsilon_2 \sigma_2] - \varepsilon_2 \phi (1 - \psi) Z_{1D}^*}. \quad (36)$$

1050

1051 Similarly, for $\gamma = 1$, $f_2 = 0$ and $f_3 = 0$ provide relationships for P that must be reconciled; $f_2 = 0$
 1052 gives:

$$1053 \quad P_D^* = \frac{\phi Z_{2D}^* + \sigma_1 (1 + \varepsilon Z_{1D}^*) Z_{1D}^*}{(1 + \varepsilon Z_{1D}^*) [\varphi_1 (1 - \psi_1) - \varepsilon_1 \sigma_1 Z_{1D}^*] - \varepsilon_1 \phi Z_{2D}^*}, \quad (37)$$

1054 and $f_3 = 0$ gives:

$$1055 \quad P_D^* = \frac{\sigma_2 (1 + \varepsilon Z_{1D}^*) Z_{2D}^* - \phi (1 - \psi) Z_{1D}^*}{(1 + \varepsilon Z_{1D}^*) [\varphi_2 (1 - \psi_2) - \varepsilon_2 \sigma_2 Z_{2D}^*] - \varepsilon_2 \phi (1 - \psi) Z_{1D}^*}. \quad (38)$$

1056 When reconciled, equations (35) and (36), and equations (37) and (38) define Z_{2D}^* in terms of Z_{1D}^* .

1057 These relationships provide complicated expressions that must be solved iteratively and which
 1058 provide little insight into the location or sensitivity of the critical points, which we hence do not
 1059 give here.

1060

1061

Figure 1
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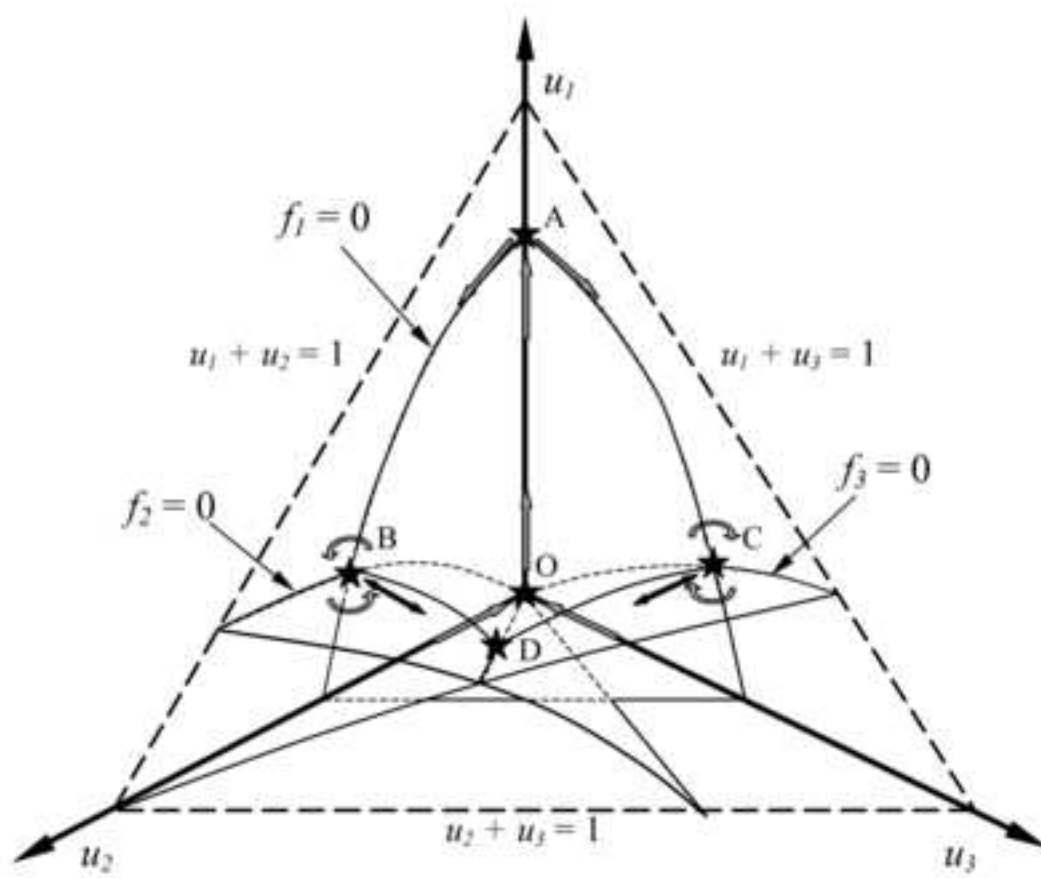


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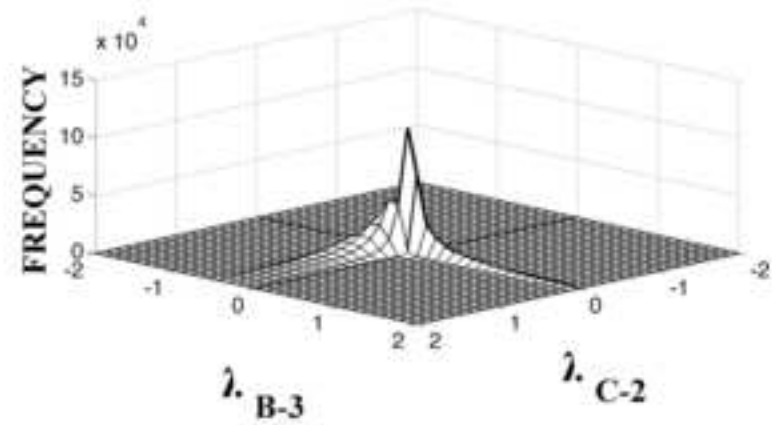
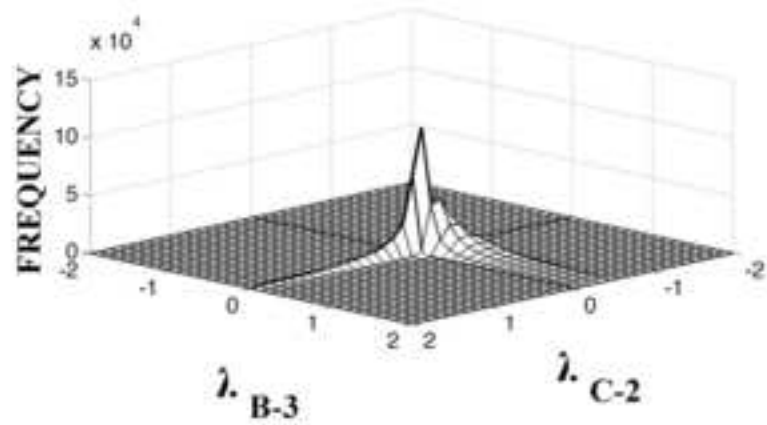
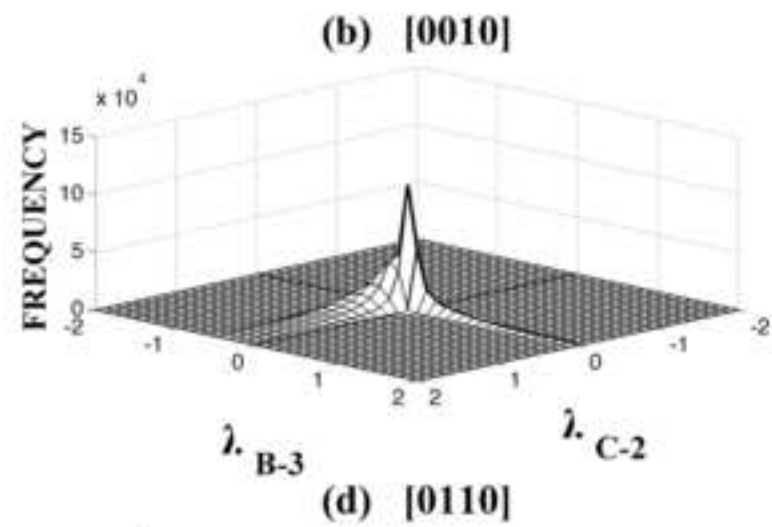
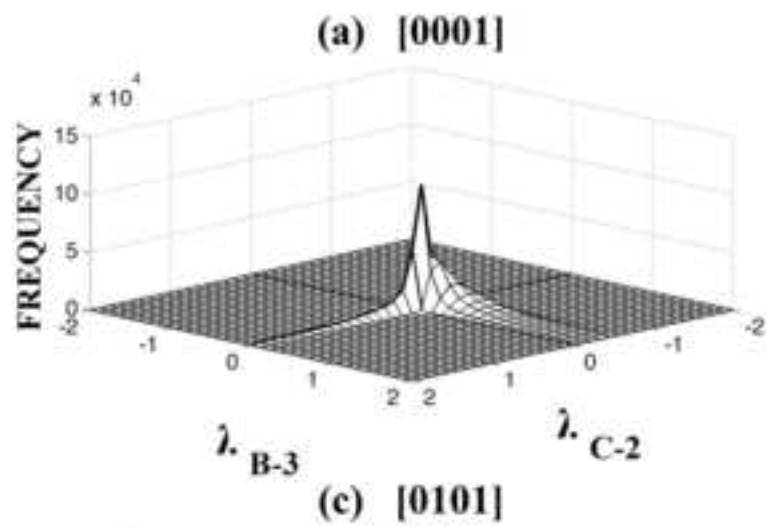


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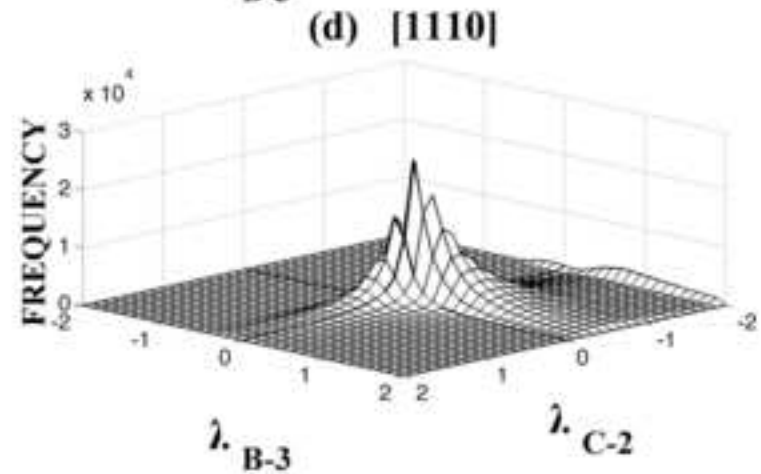
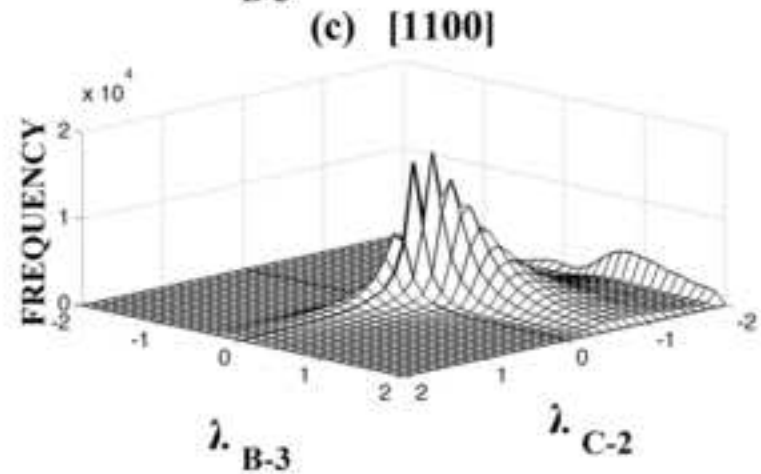
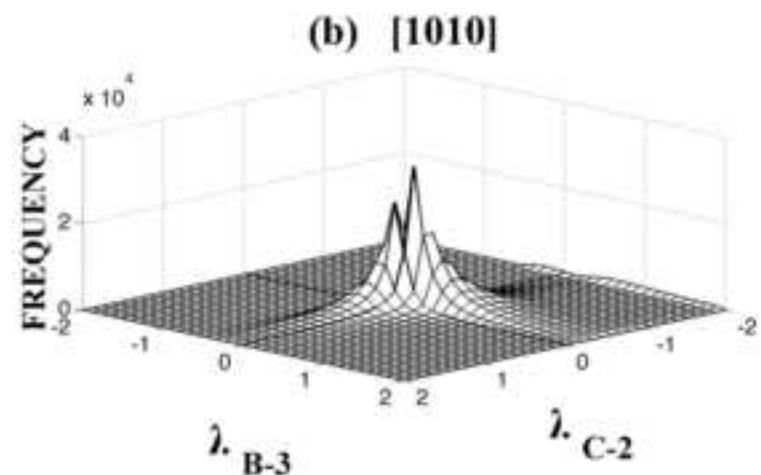
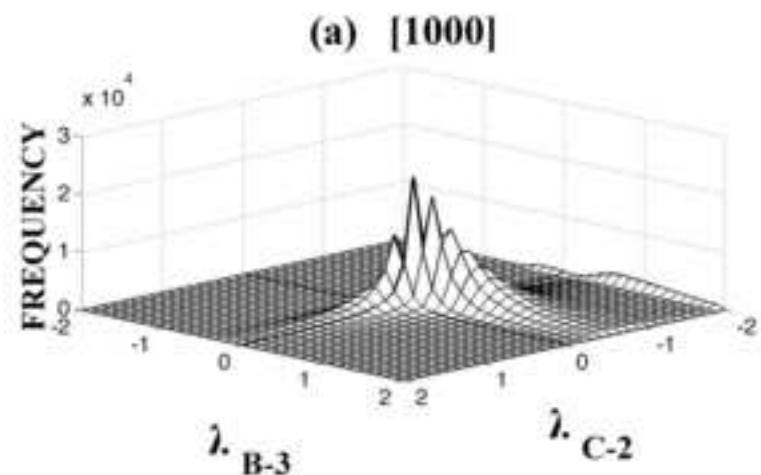


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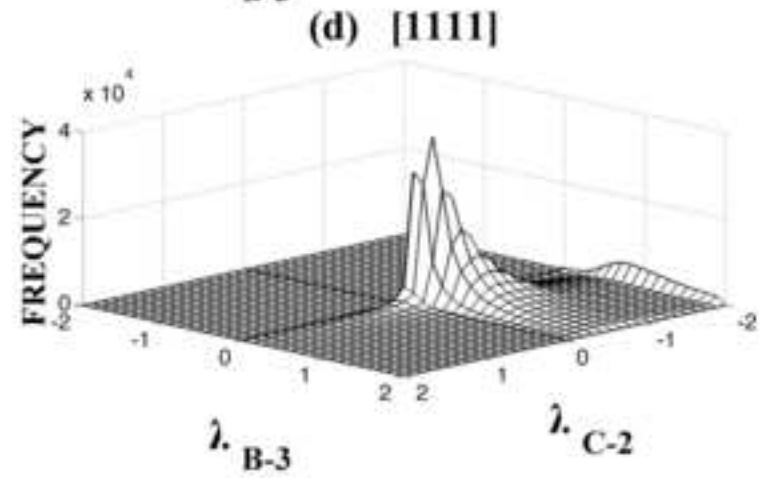
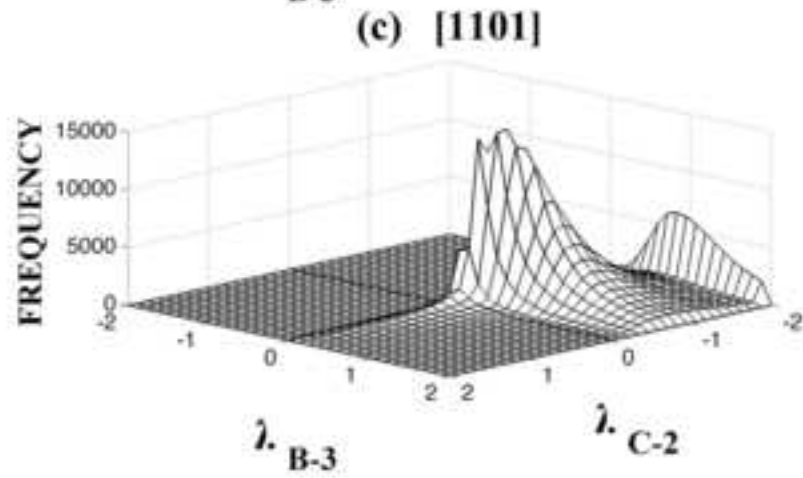
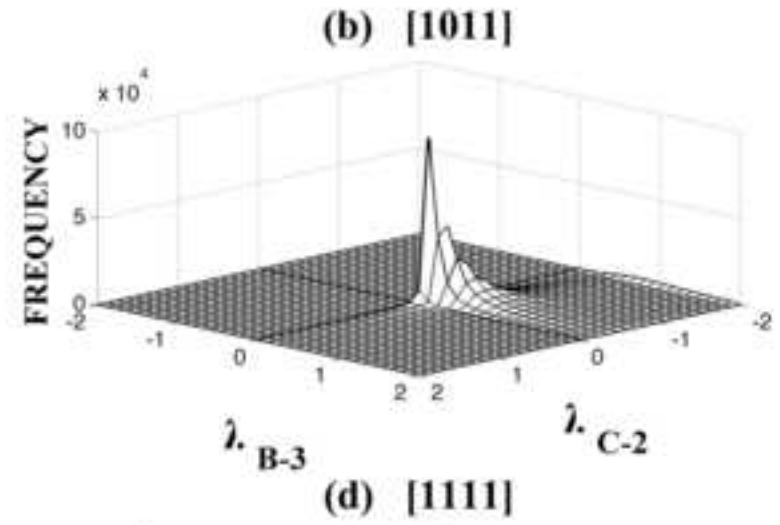
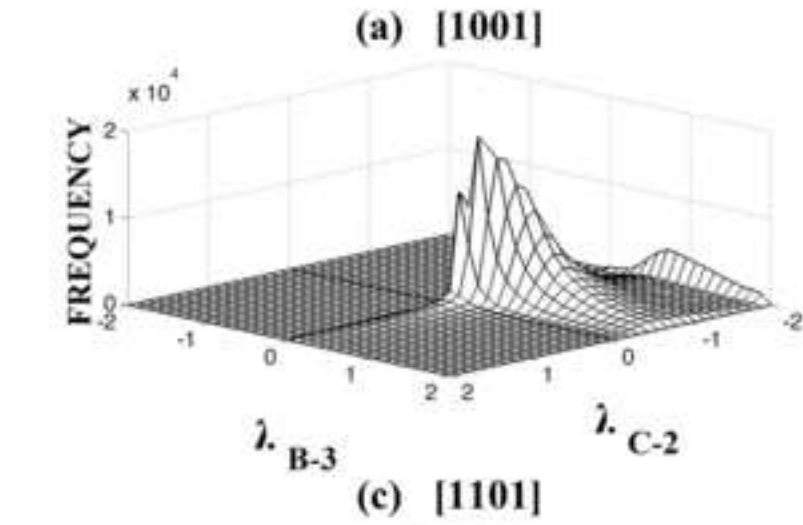


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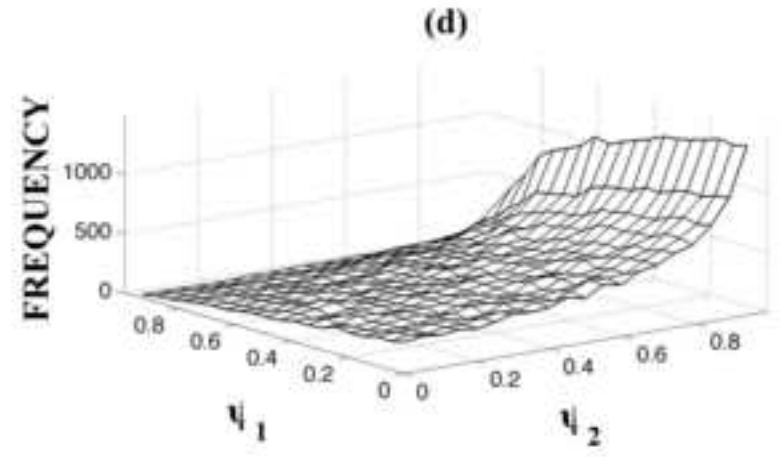
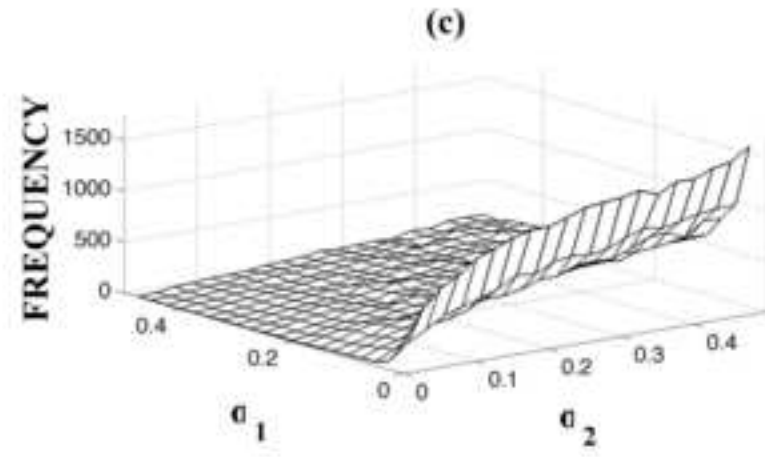
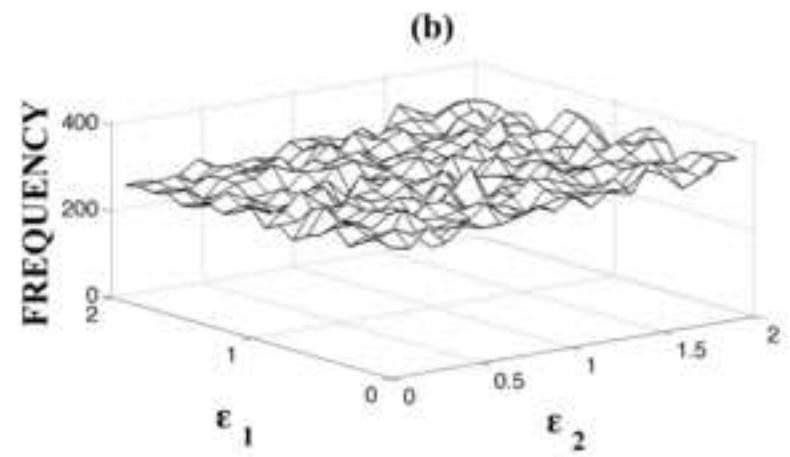
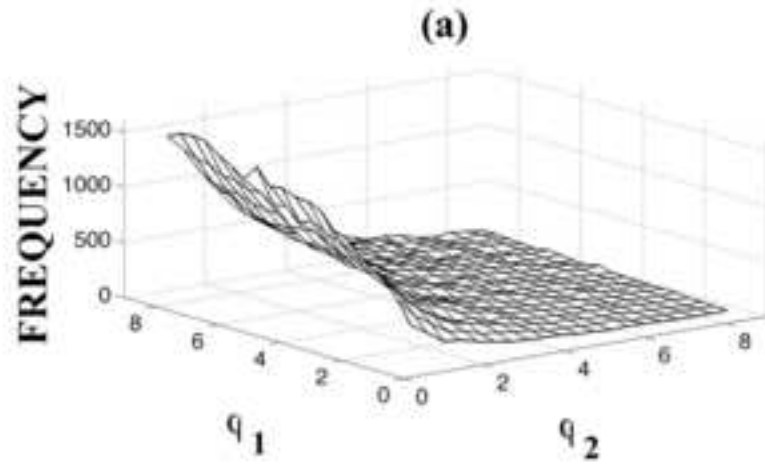


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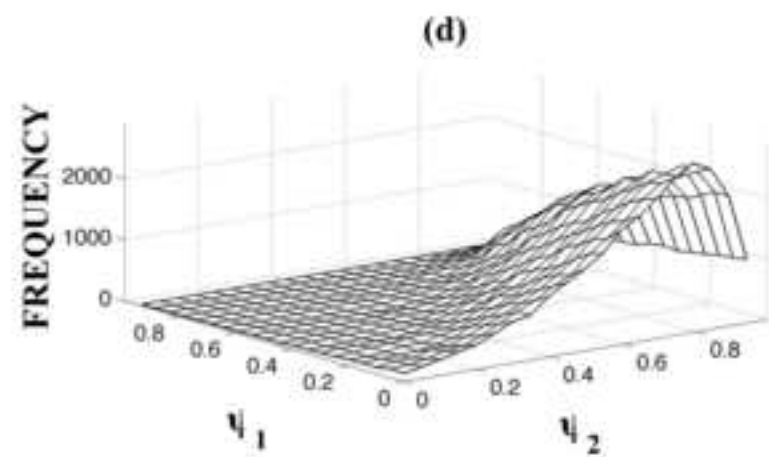
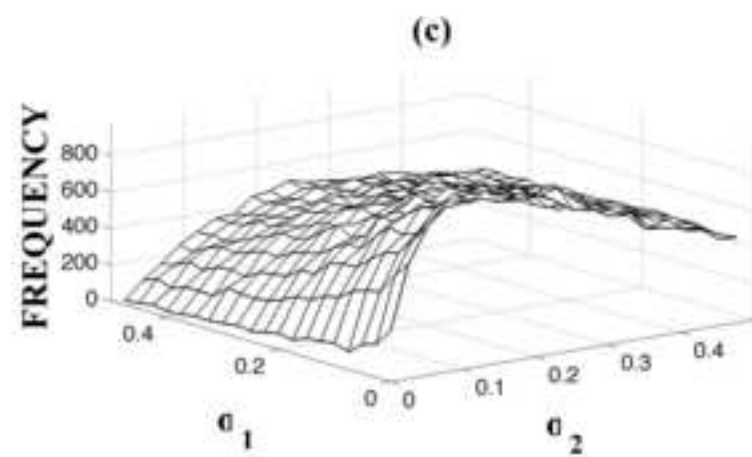
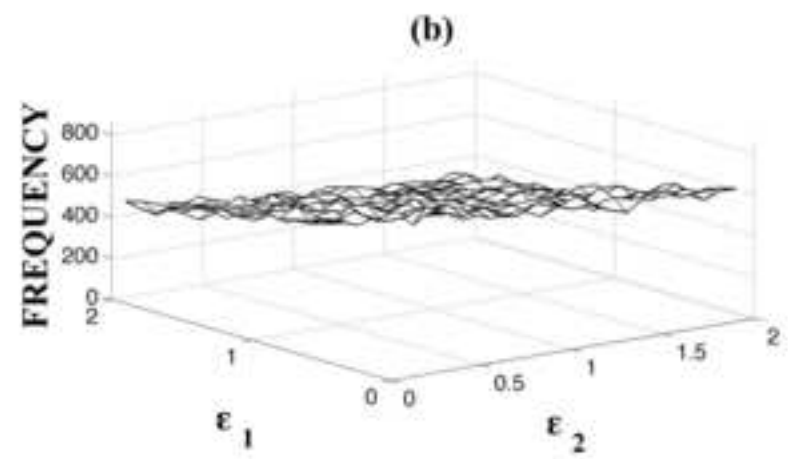
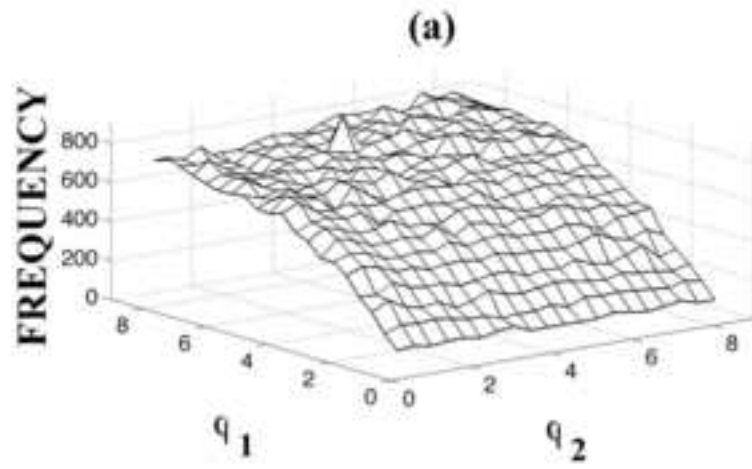


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