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Stability of complex food webs: resilience, resistance and the average interaction strength

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1 **Abstract**

2

3 In the face of stochastic climatic perturbations, the overall stability of an ecosystem will be determined
4 by the balance between its resilience and its resistance, but their relative importance is still unknown.
5 Using aquatic food web models we study ecosystem stability as a function of food web complexity.
6 We measured three dynamical stability properties: resilience, resistance, and variability. Specifically,
7 we evaluate how a decrease in the strength of predator-prey interactions with food web complexity,
8 reflecting a decrease in predation efficiency with the number of prey per predator, affects the overall
9 stability of the ecosystem. We find that in mass conservative ecosystems, a lower interaction strength
10 slows down the mass cycling rate in the system and this increases its resistance to perturbations of the
11 growth rate of primary producers. Furthermore, we show that the overall stability of the food webs is
12 mostly given by their resistance, and not by their resilience. Resilience and resistance display opposite
13 trends, although they are shown not to be simply opposite concepts but rather independent properties.
14 The ecological implication is that weaker predator-prey interactions in closed ecosystems can stabilize
15 food web dynamics by increasing its resistance to climatic perturbations.

16

17 **1 Introduction**

18 The ability of an ecosystem to return to its reference state after a perturbation stress is given by its
19 resilience (May, 1974; Harwell et al., 1977; Pimm, 1982). A high resilient ecosystem is one that is able
20 to recover fast after imbalances in the populations densities induced by climatic fluctuations. The ability
21 of an ecosystem to resist displacement from its reference state during a perturbation stress is given by
22 its resistance (Webster et al., 1975; Harwell et al., 1977; Harrison, 1979). A high resistant ecosystem is
23 one which is displaced slightly after imbalances in the populations rates induced by climatic fluctuations
24 (Harrison, 1979; Harrison and Fekete, 1980). Both properties will influence how close an ecosystem
25 remains to its reference equilibrium state and the ecosystem's variability in the face of stochastic climatic
26 perturbations. In other words, resilience and resistance are complementary properties that will determine
27 the overall stability of the ecosystem (Ives and Carpenter, 2007).

28 Ecosystem resilience has been extensively studied and it is probably the most widely used metric for
29 food web stability (May, 1972; Pimm, 1982, 1984; Loreau et al., 2002). The theory of Lyapunov stability
30 predicts that ecosystems of higher complexity should be less stable in the face of perturbations (May,
31 1974). In this regard, systems are deemed L-stable when the density of all species returns to equilibrium
32 following a perturbation (Pimm, 1982, 1984). Both the probability of displaying L-stable dynamics and
33 the rate of recovering from a perturbation in population densities have been shown to decrease with
34 ecosystem complexity in models (May, 1974; Fussmann and Heber, 2002; Chen and Cohen, 2001b; Ives
35 and Carpenter, 2007).

36 Despite the importance of resistance for ecosystem stability (Pimm, 1984), theoretical works that address
37 ecosystem resistance are much less abundant than in the case of resilience, probably due to the lack of
38 a unified theory (Harrison, 1979). Therefore, resistance has been a stability property more difficult to
39 quantify (Harwell et al., 1977; Webster et al., 1975; Harrison and Fekete, 1980; Loreau and Behera,
40 1999). Also, there is not yet a clear picture of how ecosystem resistance may be affected by food
41 web diversity (Loreau and Behera, 1999). Nevertheless, there is some empirical evidence of increased
42 resistance to environmental perturbations (e.g. drought) with biodiversity in natural grasslands (Tilman

43 and Downing, 1994; Tilman, 1996).

44 It is well known that resilience is a property that characterizes the ecosystem as a whole (Loreau and
45 Behera, 1999). However, contrary to previous suggestions that resistance is a property that characterizes
46 each ecosystem component separately (Harrison and Fekete, 1980; Loreau and Behera, 1999), resistance
47 is also a property that characterizes the ecosystem as a whole. In a euclidean multi-dimensional space
48 (e.g. multi-species ecosystem), both resilience and resistance can be measured in an analogous way from
49 the time needed to go from one point to another point in that space during the event of single climatic
50 perturbation.

51 Due to stochastic environmental fluctuations, populations in real ecosystems are almost never able to
52 remain close to their equilibrium densities (Ives, 1995). However, disentangling resilience and resistance
53 individually for stochastic ecosystems can be challenging. Resilience is a measure of the ecosystem
54 stability to fluctuations in the population densities due to environmental perturbations (Harrison, 1979).
55 It does not give, however, any information about how hard it might be for the environment to make these
56 populations fluctuate. Resistance, on the other hand, is a measure of the ecosystem stability to fluctu-
57 ations in the population rates (e.g. specific growth or mortality) (Harrison, 1979). Thus, it tells how
58 difficult it is for the environmental perturbations to make the populations fluctuate.

59 The main objective of this work is to evaluate whether equilibrium stability properties (i.e. resilience
60 and resistance) can be related to stochastic stability measures (i.e. population variability) and what
61 mechanisms are likely to explain the observed relationship between ecosystem complexity and overall
62 stability.

63 Ecosystem resilience to perturbations has been shown to depend negatively on the number of species
64 in a food web and the strength of competitive interactions between the species (May, 1972, 1974) and
65 positively on the speed of mass cycling through the system (DeAngelis, 1980; DeAngelis et al., 1989).
66 Equilibrium theory suggests that an increase in species richness and connectance should decrease the
67 resilience of ecosystems because the inter-specific competition between species are destabilizing forces
68 that will tend to push some species to extinction (May, 1974; McCann et al., 1998). However, the

69 presence of weak interactions in complex food webs has been suggested to help sustain high ecosystem
70 diversity (Kokkoris et al., 2002; Neutel et al., 2007).

71 Natural communities tend to display skewed distributions of the interaction strengths towards weak links,
72 i.e. many weak interactions and few strong ones (Paine, 1992; McCann et al., 1998; Neutel et al., 2002,
73 2007), although the underlying mechanisms are not completely well understood (Berlow et al., 2004).
74 Among them, the number of prey per predator seems to correlate to the strength of the interactions;
75 polyphages (i.e. predators with many prey) have weaker predator-prey interactions than monophages
76 (McCann et al., 1998; Montoya et al., 2006).

77 Little is known about the dependence of resistance on ecosystem complexity, species interaction strength
78 and the rate of mass cycling through the food web. Therefore, it is unknown what determines the resis-
79 tance of ecosystems to climatic perturbations. It is also unknown what is the relative weight of resilience
80 and resistance on the overall stability of stochastic ecosystems.

81 We address these questions by means of multi-species food web models that are mass-conservative (i.e.
82 closed ecosystems). Specifically, we evaluate how a decrease in the strength of predator-prey interactions
83 with food web complexity will affect ecosystem resilience, resistance and overall stability. We will use as
84 climatic perturbations drastic changes in solar radiation levels (i.e. dark/light pulses). They will therefore
85 affect the specific growth rate of primary producers.

86 Food web resilience and resistance will be evaluated by applying a single perturbation (i.e. one dark
87 pulse) to the ecosystems. Resistance will be measured as the time needed to reach a given non-equilibrium
88 perturbed state from the reference equilibrium state. Resilience will be measured as the return rate from
89 the non-equilibrium perturbed state back to the reference equilibrium state. Food web overall stability
90 will be evaluated by applying a stochastic perturbation (i.e. many random dark pulses) to the ecosystems.

91 We will define a metric for overall stability that merges both the temporal variability of the system and its
92 average distance to the reference state, and we will compare it to more classical measures of ecosystem
93 variability such as the coefficient of variation of population-level, community-level and ecosystem-level
94 properties.

95 2 Methodology

96 2.1 Model description

97 We constructed a series of food web models that differ in their complexity. Food web complexity here
98 refers to the number of plankton species or plankton functional types (PFT) (Le Quéré et al., 2005). A
99 minimum of 3 and a maximum of 6 trophic levels is considered. Complexity increases along two axis in
100 the model: 3 levels of phytoplankton complexity (p-cmpx) and 4 levels of zooplankton complexity (z-
101 cmpx). Therefore there are 12 food web configurations between the least and most complex ecosystem.
102 The most complex food web is based on the schematic food web described by Duffy et al. (2007). The
103 least complex model is a short linear food web. Model equations are given in Box 1 and Box 2. Model
104 equation terms are listed in Table 1. Parameter values are listed in Table 2. The topology diagrams for
105 the 12 food web complexities is given in Figure 1. Note that all food web complexities can be generated
106 as substructures of the most complex food web. For phytoplankton we chose to go from large to small
107 when increasing p-cmpx, but we obtain analogous results if we go from small to large phytoplankton (see
108 Supp.Mat). For zooplankton we go from lower trophic to higher trophic levels when increasing z-cmpx.

109 Primary production is limited by the availability of dissolved inorganic nitrogen (DIN) following Michaelis-
110 Menten nutrient uptake kinetics. Predation is assumed to follow a Holling-Type III (sigmoid) functional
111 response, which is common in filter feeders and marine copepods (Jeschke et al., 2004; Fussmann et al.,
112 2005). Type III functional responses for predation are known to stabilize model dynamics and to promote
113 biodiversity through a relaxation of feeding at low prey densities, allowing for a much greater probability
114 of co-existence of all the species in a food web (Haydon (1994); Gentleman et al. (2003); and references
115 therein). The use of functional relationships including a relaxation of feeding at low prey densities is
116 a way of implicitly taking into account several ecological mechanisms like prey refuge, prey switching
117 and/or predator interference that are difficult to model explicitly. Alternatively, one can make use of
118 Holling-Type II functional response with an explicit refuge for the prey. In any case, our results are not
119 dependent on this choice (see Supp.Mat). Fish (top carnivore) is used in the model simply as a closure

120 mortality term for zooplankton. All losses (i.e. mortality, non-assimilated food) are assumed to be in-
121 stantaneously recycled to the nutrients DIN pool, making the ecosystem mass-conservative. The total
122 amount of mass in the system is constant and it is the same for all food web configurations ($N_{tot} = 2$
123 mmolN m^{-3}).

124 The strength of zooplankton predation upon their prey is assumed to decrease with the number of prey
125 per predator (McCann et al., 1998; Montoya et al., 2006). Therefore, the model assumes that pressure
126 on individual prey decreases when predators scavenge multiple prey. This can be understood as a way
127 of implicitly reflecting an increase in the predators difficulty to attack their prey due to an increase in
128 habitat complexity with species diversity (Real, 1977), such as heterogeneities in prey distribution (i.e.
129 patches) or prey defense-strategies, which are not explicitly accounted for in the model. The decrease in
130 predator-prey interaction strength comes from two complementary mechanisms. First, we assume that
131 an increase in the number of prey per predator decreases the predator's efficiency in capturing any of its
132 prey, which is parametrized as an increase in the predator's half-saturation constant for ingestion (eq(10)
133 gives the predation efficiency as a function of the number of prey). This might be seen as a transition
134 from a highly efficient specialist to a low efficiency generalist, or it can reflect an increase in the average
135 transit time spent from going from one prey type patch to another (Oaten, 1977). Second, since each
136 prey has its own implicit grazing refuge in the Type III functional response (or explicit if using Type II
137 with refuge), the presence of more prey types implies a higher overall refuge for the prey as a whole.
138 Both mechanisms will tend to decrease the average interaction strength between predators and prey as
139 food web complexity increases.

140 The modelled PFTs were allowed to differ in their phenotypic traits for the exploitation of resources.
141 Both the phytoplankton maximum growth rates and nutrient half-saturation constants, as well as the
142 zooplankton maximum ingestion rates and half-saturation constants for ingestion, are assigned randomly
143 from a normal distribution with mean values given in Table 2 and a standard deviation of 0.2 times the
144 mean value. In practice this means a range for parameter values of approximately $\pm 50\%$ the mean
145 values. (Using a uniform distribution with a range $\pm 50\%$ the mean values gave similar results). For
146 each of the 12 food web complexities we performed 400 runs with randomly-assigned phenotypic traits.

147 This amounts to a total of $12 \times 400 = 4800$ individual runs. We also performed an extra run in which
148 all phytoplankton and all zooplankton share the same traits respectively (i.e. parameter values given in
149 Table 2) which will be the control run for a parameters' sensitivity analysis (see Supp.Mat). For all runs
150 the ecosystems have a single L-stable reference equilibrium under constant light levels, regardless of the
151 initial conditions. Therefore, all food web complexities are globally L-stable (Pimm, 1982; Chen and
152 Cohen, 2001a).

153 **2.2 Dynamical Stability Indices**

154 The only external forcing in the model is solar radiation. Therefore, we will use as climatic perturbations
155 dark-pulses in solar radiation levels. The ecosystems will be allowed to be under only two possible
156 environmental conditions: perturbed (full dark) or unperturbed (full light). Three dynamical stability
157 indices (DSI) will be computed numerically: resilience, resistance, and overall stability. Resilience and
158 resistance will be estimated by applying a single perturbation (i.e. one dark pulse) to the ecosystems.
159 Overall stability will be evaluated by applying a stochastic perturbation (i.e. many random dark pulses)
160 to the ecosystems.

161 **2.2.1 Resilience Index**

162 The reference steady-state point (SSP), or unperturbed equilibrium, is the point \mathbf{X}^* with coordinates
163 (X_1^*, \dots, X_n^*) in the phase space in which the concentration of the PFTs does not change over time. Since
164 all our model food webs are globally Lyapunov stable, any departure from the reference state caused by
165 a climatic perturbation will decay over time once the perturbation has ceased, and the ecosystems will
166 asymptotically return back to their reference equilibrium. The resilience of the systems will be estimated
167 by measuring the time needed for recovery, and then converting the return times into return rates. This
168 has the advantage of giving a comparable measure to the dominant eigenvalue of the Jacobian matrix
169 (May, 1974).

Model equations

- *Phytoplankton* [mmolN m^{-3}]

$$\frac{\partial P_i}{\partial t} = F_{P_i} - G_{P_i Z} - M_{P_i} \quad (1)$$

- *Zooplankton* [mmolN m^{-3}]

$$\frac{\partial Z_j}{\partial t} = F_{Z_j} - G_{Z_j Z} - G_{Z_j C} - M_{Z_j} \quad (2)$$

- *Top Carnivore Fish* [mmolN m^{-3}]

$$\frac{\partial C}{\partial t} = F_C \cdot \left(1 - \frac{C}{K_C}\right) - M_C \quad (3)$$

- *Dissolved Inorganic Nutrients* [mmolN m^{-3}]

$$\frac{\partial \text{DIN}}{\partial t} = - \sum_i^m F_{P_i} + \sum_i^m M_{P_i} + \sum_j^n E_{Z_j} + \sum_j^n M_{Z_j} + E_C + F_C \cdot \frac{C}{K_C} + M_C \quad (4)$$

Model terms

- *Phytoplankton production (F_{P_i})*

$$F_{P_i} = \mu_{P_i} \cdot Q_{P_i}^{DIN} \cdot Q_{P_i}^{PAR} \cdot P_i \quad (5)$$

$$Q_{P_i}^{DIN} = \frac{DIN}{k_{P_j} + DIN} \quad (6)$$

$$Q_{P_i}^{PAR} = (*) \quad (7)$$

(*) = 1 or 0 (unperturbed / perturbed)

- *Zooplankton grazing / predation ($G_{X_i Z_j}$)*

$$G_{X_i Z_j} = g_{Z_j} \cdot Z_j \cdot \frac{X_i^2}{(k_{Z_j} / \varepsilon_{Z_j})^2 + \sum_i^m X_i^2} \quad (8)$$

$$G_{X_i Z} = \sum_j^n G_{X_i Z_j} \quad (9)$$

$$\varepsilon_{Z_j} = \frac{1}{m^\alpha} \quad (10)$$

- *Zooplankton production (F_{Z_j}) and excretion (E_{Z_j})*

$$F_{Z_j} = \beta_Z \cdot \sum_i^m G_{X_i Z_j} \quad (11)$$

$$E_{Z_j} = (1 - \beta_Z) \cdot \sum_i^m G_{X_i Z_j} \quad (12)$$

- *Top Carnivore Fish predation ($G_{Z_j C}$)*

$$G_{Z_j C} = g_C \cdot C \cdot \frac{Z_j^2}{k_C^2 + \sum_j^n Z_j^2} \quad (13)$$

- *Top Carnivore Fish production (F_C) and excretion (E_C)*

$$F_C = \beta_C \cdot \sum_j^n G_{Z_j C} \quad (14)$$

$$E_C = (1 - \beta_C) \cdot \sum_j^n G_{Z_j C} \quad (15)$$

- *Natural mortality of phytoplankton (M_{P_i}), zooplankton (M_{Z_j}) and top carnivore fish (M_C)*

$$M_{P_i} = m_P \cdot (1 - e^{-\gamma_P \cdot P_i}) \cdot P_i \quad (16)$$

$$M_{Z_j} = m_Z \cdot (1 - e^{-\gamma_Z \cdot Z_j}) \cdot Z_j \quad (17)$$

$$M_C = m_C \cdot (1 - e^{-\gamma_C \cdot C}) \cdot C \quad (18)$$

172 We define a perturbation as the period over which solar radiation is set artificially to zero (dark-pulse)
 173 until the system reaches a perturbed non-equilibrium state $\mathbf{X}(\mathbf{t}) = \mathbf{X}^* + \mathbf{x}(\mathbf{t})$, where $\mathbf{x}(\mathbf{t})$ is a given
 174 perturbation distance. The distance between the perturbed point and the steady-state point is given by
 175 the classical Euclidean norm (Neubert and Caswell, 1997):

$$\mathbf{x}_t \equiv \|\mathbf{x}(\mathbf{t})\| = \sqrt{x_1^2(t) + x_2^2(t) + \dots + x_n^2(t)} = \sqrt{\sum x_i^2(t)} \quad (19)$$

176 The maximum potential distance is given by the distance between an extreme unperturbed point in which
 177 the total mass N_{tot} in the system is allocated in a single PFT, and an extreme perturbed point in which
 178 all PFT concentrations tend to zero so that the nutrients pool in the system tends to N_{tot} . Therefore:

$$\mathbf{x}_0^{\max} \equiv \|\mathbf{x}(\mathbf{0})\|^{max} = \sqrt{N_{tot}^2 + 0 + \dots + N_{tot}^2} = \sqrt{2 \cdot N_{tot}^2} \approx N_{tot} \quad (20)$$

179 The dark-pulse perturbation will be in place until a given 10% of the maximum potential distance be-
 180 tween the perturbed point and the steady-state point was attained (i.e. $\mathbf{x}_0 = \delta_0 \cdot \mathbf{x}_0^{\max}$; with $\delta_0 = 0.1$).
 181 Then full light conditions will be back again and we will numerically compute the time needed by the
 182 system to recover ($\delta' < \delta_0$) to a 99.99% level. From the return times we can calculate the return rates
 183 [d^{-1}] assuming an exponential decay of the perturbation distance:

$$\mathbf{x}_{t'} = \mathbf{x}_0 \cdot e^{\eta \cdot t'} \quad (21)$$

184 where \mathbf{x}_0 is the perturbation distance, $\mathbf{x}_{t'}$ is the return distance, t' is the return time, and η is the return
 185 rate. Making these distances a fraction of the maximum potential distance of a perturbation:

$$\delta' \cdot \mathbf{x}_0^{\max} = \delta_0 \cdot \mathbf{x}_0^{\max} \cdot e^{\eta \cdot t'} \quad (22)$$

$$\delta' = \delta_0 \cdot e^{\eta \cdot t'} \quad (23)$$

186 Taking the logarithm on both sides and isolating η , we obtain the resilience index:

$$\eta = \frac{\ln(\frac{\delta'}{\delta_0})}{t'} \quad (24)$$

187 2.2.2 Resistance Index

188 The resistance of the ecosystems to the dark-pulse perturbation was measured as the perturbation time
189 (the length of the dark-pulse), i.e. the time needed by the system under the influence of the dark-pulse to
190 reach the selected perturbation distance. Longer perturbation times imply a slower displacement per unit
191 of time and thus a higher resistance to the perturbation (Harrison, 1979).

192 The ultimate displacement is the distance between the “all alive” reference equilibrium state and the
193 “all died” equilibrium state that would occur if the disturbance lasted indefinitely (Harrison and Fekete,
194 1980). Although the ultimate displacement can be different for each ecosystem depending on the coor-
195 dinates of its reference state, it can be shown that the differences are negligible and all the modelled food
196 webs have similar ultimate displacements that are, in fact, very close to the maximum potential distance
197 (i.e. N_{tot}). Therefore, the measured perturbation time is a dynamical resistance index related to the speed
198 at which the ecosystems depart from the reference state towards its ultimate displacement.

199 2.2.3 Stability Index

200 To obtain an estimate of the overall stability of the food webs, we performed a simulation in which the
201 ecosystems were submitted to a stochastic perturbation of light levels (i.e. dark/light pulses) during one
202 year without seasonality. Each day had a probability of 50% to be assigned a zero light level. For those
203 random dark-days, phytoplankton do not grow (perturbed states). For all the other days, phytoplankton
204 growth was not light-limited (unperturbed states). The severity of every perturbation is given by the
205 amount of consecutive dark-days. Prior to the start of the stochastic perturbation each food web was
206 allowed to reach its reference equilibrium state after a year under no light-limited growth.

207 Ecosystems under stochastic perturbations are always in a non-equilibrium state (Ives, 1995). Every
 208 time that a perturbation comes in, the system moves away from its reference equilibrium state; once
 209 the perturbation is gone, the system moves back towards its reference equilibrium state. Since there is
 210 never enough time to fully recover before another perturbation comes in, the system is unable to reach
 211 the steady-state. Under those conditions the equilibrated state can be given by a stationary distribution
 212 characterized by its mean and standard deviation (Ives et al., 2003). Specifically we will use the tra-
 213 jectories in the phase space, evaluated with respect to the reference equilibrium (i.e. displacements), as
 214 the stationary distribution of the stochastic system. The mean of the stationary distribution measures the
 215 average distance to the reference equilibrium. The standard deviation measures the temporal variability
 216 of the distances.

217 We will show that the distances between the stochastic non-equilibrium states and the reference equilib-
 218 rium state do not follow a normal distribution. They are best described by a Weibull distribution, which
 219 is characterized by two parameters: the shape and the scale parameter (Rinne, 2008). We fit a Weibull
 220 probability density function (PDF) to the stochastic distances, and then calculated the mean (μ) and stan-
 221 dard deviation (σ) of the Weibull distribution (Rinne, 2008). (The only restriction imposed on was that
 222 the shape parameter had to be ≥ 1.25 to avoid exponential distributions.) Low mean and low standard
 223 deviation of the stationary distribution means high stability of the stochastic ecosystem. We now define
 224 the parameter φ as the square root of the product between the mean and the standard deviation of the
 225 stationary Weibull distribution:

$$\varphi = \sqrt{\mu \cdot \sigma} \quad (25)$$

226 We use the inverse of parameter φ of the Weibull PDF as the overall stability index:

$$\xi = \frac{1}{\varphi} \quad (26)$$

227 2.3 Average Interaction Strength

228 To measure the strength of species interactions we obtained the Interaction matrix from the Jacobian
 229 matrix computed at the reference equilibrium (Berlow et al., 2004). The elements c_{ij} in the Interaction
 230 matrix give the linear effect of a small change in the concentration of species j on the specific (i.e.
 231 *per-capita*) rate of change of species i :

$$c_{ij} = \left. \frac{\partial(\dot{X}_i/X_i)}{\partial X_j} \right|_{\mathbf{X}^*} \quad (27)$$

232 where \dot{X}_i denotes the rate of change of species i and X_i its concentration. The ecosystem average
 233 interaction strength (EAIS) was obtained from the absolute value of the off-diagonal elements in the
 234 Interaction matrix:

$$\mathbf{EAIS} = \frac{\sum_{i \neq j}^n |c_{ij}|}{n(n-1)} \quad (28)$$

235 where n is the total number of species in the food web. Note that the interactions with nutrients were not
 236 included in the calculations.

237 We chose to use the elements of the Interaction matrix [$\text{m}^{-3} \text{mmolN}^{-1} \text{d}^{-1}$] (Kokkoris et al., 1999) over
 238 the elements in the Jacobian matrix [d^{-1}] (Neutel et al., 2002) because they give per-capita interaction
 239 strengths, i.e. equivalent to the interaction coefficients in the Lotka-Volterra model (Wootton, 1997), and
 240 therefore measure a level of interaction between species that is independent of the equilibrium concen-
 241 trations, which may change from one food web to another. This provides a more objective measure of
 242 the imposed decrease in species interaction with complexity, since variations in interaction strength re-
 243 sulting from differences in species' densities are circumvented (Laska and Wootton, 1998). This metric
 244 has been extensively used to study the stability of both real food webs (Emmerson and Raffaelli, 2004)
 245 and ecosystem models (Kokkoris et al., 1999; Jansen and Kokkoris, 2003). In any case, using instead the
 246 elements in the Jacobian to measure the strength of species interactions did not change significantly the
 247 results since the correlation between average Jacobian Matrix strength and average Interaction Matrix
 248 strength is very high (see Supp.Mat).

249 **3 Results**

250 In this section we will show the relationship between the ecosystems' state, productivity and stability
251 properties as a function of the food web complexity, which is defined along two axis as the number of
252 phytoplankton and zooplankton species present in each food web (p-cmpx and z-cmpx, respectively; see
253 methods). For each of the 12 food web complexities, we take the average of 400 runs with randomly-
254 assigned phenotypic traits.

255 Figure 2 shows the steady-state concentrations as a function of phytoplankton and zooplankton com-
256 plexity. Total phytoplankton biomass increases (about a 70%) along its own phytoplankton complexity
257 (p-cmpx) axis from ≈ 0.7 to ≈ 1.2 mmolN m^{-3} , but remains almost unchanged along the zooplankton
258 complexity (z-cmpx) axis. Total zooplankton biomass decreases (about a 30%) along the phytoplank-
259 ton complexity axis from ≈ 1.0 to ≈ 0.70 mmolN m^{-3} , but slightly increases (about 15%) along its own
260 zooplankton complexity axis. Top carnivore fish biomass displays a moderate decrease both along the
261 phytoplankton and zooplankton complexity axes (about a 30-40%), going from ≈ 0.25 to ≈ 0.10 mmolN
262 m^{-3} between the simplest and most complex food web. Finally, dissolved inorganic nutrients (DIN) also
263 decreases both along the phytoplankton (about a 80%) and zooplankton (about a 40%) complexity axes,
264 going from ≈ 0.2 to ≈ 0.01 mmolN m^{-3} between the simplest and most complex food web. This implies
265 a higher degree of retention of nutrients by the organisms with food web complexity.

266 The increase of total phytoplankton along the p-cmpx axis can be mainly attributed to the imposed lower
267 predation pressure upon phytoplankton when more species are added. For the same reason, this increase
268 is mirrored by a small decrease in total zooplankton along the p-cmpx axis. Along the z-cmpx, however,
269 since zooplankton can be at the same time both predator and prey, the lower food intake is balanced by a
270 lower predation mortality and therefore the total zooplankton increase is much smaller.

271 Figure 3 gives the rate of mass input fluxes between compartments at the reference steady-state as a
272 function of phytoplankton and zooplankton complexity. Between the simplest and most complex food
273 web, primary production decreases by more than 50% (from ≈ 0.4 to ≈ 0.2); zooplankton production

274 decreases by more than 60% (from ≈ 0.12 to ≈ 0.04); fish production decreases by more than 80% (from
275 ≈ 0.03 to ≈ 0.005); and the recycling production of DIN decreases about 70% (from ≈ 0.9 to ≈ 0.3).

276 Thus, although the degree of retention of nutrients increases with food web complexity (Figure 2d), the
277 rate of instantaneous production in the system decreases (Figure 3) due to the imposed weaker predator-
278 prey interactions when more species are added. Weaker predator-prey interactions means slower recy-
279 cling of DIN from zooplankton excretion, slowing down the pace of phytoplankton primary production.
280 Thus, assuming that predator-prey interactions are weaker with more prey choices results in a decrease
281 with food web complexity of the speed of mass cycling in the ecosystem.

282 Figure 4a gives the ecosystems' average interaction strength as a function of phytoplankton and zoo-
283 plankton complexity. The EAIS decreases strongly along both axes, which is to be expected since the
284 model assumes a general decrease in the predator-prey interactions with food web complexity. The av-
285 erage interaction goes from ≈ 0.25 to ≈ 0.1 between the simplest and most complex food web, about a
286 60% decrease. Figures 4b,c,d give the food webs' DSI: resilience, resistance, and overall stability; re-
287 spectively. We found that resilience decreases (about 75%) with food web complexity (Figure 4b), with
288 the rate of return (i.e. 99.99% recovery) going from ≈ 0.2 to ≈ 0.08 [d^{-1}] between the simplest and most
289 complex food web. On the other hand, resistance increases (about a 200%) with food web complexity
290 (Figure 4c), with the perturbation time going from ≈ 0.4 to ≈ 1.2 [d] between the simplest and most com-
291 plex food web. This means that in order to displace the ecosystems the same perturbation distance (see
292 section 2.2.1), the most complex food web can resist the climatic perturbation 3 times longer than the
293 simplest one. The overall stability also increases (about a 200%) with food web complexity, going from
294 ≈ 3.0 to ≈ 9.0 [$m^3 \text{ mmolN}^{-1}$] between the simplest and most complex food web. The similarity between
295 how the resistance index and the stability index change with food web complexity is apparent, which
296 already indicates that the overall stability of the food webs seems more related to their resistance than to
297 their resilience.

298 Figure 5 shows the probability density functions of the distances between the stochastic ecosystem and
299 the reference equilibrium for each level of phytoplankton (top-down) and zooplankton complexity (left-

300 right). We see that as food web complexity increases, both the mean and the standard deviation of
301 the Weibull PDF decrease. This means that the stochastic ecosystem remains closer to the reference
302 equilibrium and display lower temporal variability when food web complexity is higher. In other words,
303 the ecosystems' stability increases with food web complexity.

304 Figure 6 shows the dynamics of the stochastic ecosystems just for the simplest and most complex food
305 web. In this case the results are from the single control run (see methods), not the average values from
306 the random runs, since the figure is illustrative only. (Note that all the stability properties of the con-
307 trol run are almost identical to the averaged stability properties of the random runs, see Supp.Mat).
308 Figure 6a shows the trajectories in the euclidean phase space of these two stochastic ecosystems (P.Z
309 and PPP.ZZZZ). Figure 6b show the corresponding time-series. The PPP.ZZZZ stochastic ecosystem is
310 clearly more stable than the P.Z stochastic ecosystem; it displays both lower temporal variability and its
311 trajectories remain closer to the reference equilibrium.

312 Figure 7 shows the relationship between the dominant eigenvalue of the Jacobian matrix versus the
313 average interaction strength and the food webs' DSI. Of these four metrics, only the return rate (i.e.
314 the resilience index) correlates well with the dominant eigenvalue, which is to be expected since in fact
315 they are both measuring the same property (the resilience of the ecosystems). In all other cases, the
316 relationship between the resilience measured by the dominant eigenvalue versus EAIS, resistance, and
317 overall stability, shows negative but not significant trends. One important conclusion is that resilience and
318 resistance are not simply inverse concepts but rather appear to be independent properties, as previously
319 suggested (Harrison, 1979).

320 Likewise, figure 8 shows the relationship between the total primary production in the ecosystem versus
321 the average interaction strength, food webs' DSI resistance and overall stability, and the average rate
322 of mass cycling in the system (excluding primary production). All four metrics correlate strongly with
323 primary production. The correlation is positive, which means that a decrease in primary production is
324 related to a decrease in EAIS, a decrease in the speed of mass cycling, and an increase in resistance and
325 overall stability (note that the plots are against the inverse of these two stability indices).

326 Finally, figure 9 shows the relationship between the parameter φ of the Weibull distribution (i.e. the
327 inverse of the stability index) and the coefficient of variation (CV) for the individual populations of
328 phytoplankton and zooplankton species (figure 9a); the aggregated populations of total phytoplankton
329 and total zooplankton (figure 9b); the average rate of mass cycling in the system (excluding primary
330 production) (figure 9c); plus versus the parameter φ calculated using the mean and standard deviation of
331 the raw data of the stochastic displacements, i.e. without fitting a Weibull distribution (figure 9d). All
332 four metrics correlate well with parameter φ of the Weibull distribution. Again, the correlation is positive,
333 which means that an increase in the stability index (note the Weibull φ is the inverse of the stability index)
334 is related to an increase in the stability of properties at the population-level, the community-level and the
335 ecosystem-level (i.e. time-series of individual populations, aggregated populations, and mass cycling
336 rate; respectively). Also it shows that our definition of stability index is not sensitive to the choice of
337 fitting a Weibull distribution to the raw data.

338 **4 Discussion**

339 The importance of the strength of species interactions for the stability of complex ecosystem has been
340 studied extensively (Yodzis, 1981; McCann et al., 1998; Ives and Jansen, 1998; Kokkoris et al., 2002;
341 Jansen and Kokkoris, 2003; Neutel et al., 2002, 2007; Berlow et al., 2004; Emmerson and Raffaelli,
342 2004). Many works have evaluated the effect of interaction strength on the resilience of ecosystems
343 (Ives and Jansen, 1998; Neutel et al., 2002; Emmerson and Raffaelli, 2004; Neutel et al., 2007), the
344 inhibition of chaotic oscillations (McCann et al., 1998) or the vulnerability of communities to species
345 invasions (Kokkoris et al., 1999). Weaker interactions were shown to stabilize ecosystem dynamics and
346 this has been suggested to help sustain high levels of species diversity (Kokkoris et al., 2002; Neutel
347 et al., 2007). We do not find, however, a clear robust relationship between EAIS and the resilience index,
348 and if anything the trend is negative. That is, decreasing the species interaction strength with complexity
349 does not preclude the ecosystem to become less resilient. This supports previous findings that ecosystem
350 resilience decreases with food web complexity (May, 1972; Ives and Carpenter, 2007).

351 On the other hand, we are not aware of any work addressing the effect of interaction strength on the
352 resistance of complex ecosystems to climatic perturbations. Since the overall stability of an ecosystem is
353 determined by the balance between its resilience and its resistance (Harrison, 1979; Ives and Carpenter,
354 2007), it seems clear that there is a gap of knowledge about an important component of ecosystem
355 stability. We do find that a decrease of species interaction strength with complexity produces an increase
356 of ecosystem resistance, and that this promotes a higher overall stability of the system. The relationship
357 between EAIS and the resistance index, and between resistance and the overall stability, are both robust
358 and positive. That is, decreasing the species interaction strength with complexity increases the overall
359 stability of the ecosystem.

360 The mechanism that explains the increase in overall stability with ecosystem complexity is the decrease
361 in the speed of mass cycling due to the weakening of the species interaction strength with food web com-
362 plexity, which causes an increase in the ecosystem resistance. In contrast, resilience has been previously
363 suggested to increase with the rate of mass cycling through the food web (DeAngelis, 1980; DeAngelis
364 et al., 1989). While our results still support this view, they show that resilience and resistance are not just
365 exact opposite properties. We find no clear positive relationship between the rate of mass cycling through
366 the food webs and their resilience, at least not as clear as the negative relationship we find between mass
367 cycling and resistance. It turns out that other effects, like competitive interactions among species, may
368 be more important to determine the level of resilience than the mass turnover rate.

369 The reason why mass cycling rate and resistance are mechanistically connected is simple. At low cycling
370 rates the ecosystem dynamical state is one of slow motion. Therefore, it will react slowly to imbalances in
371 population parameters induced by climatic perturbations. In fact, affecting some population parameters
372 amounts to a change in the fluxes between some compartments in the system (Harrison and Fekete,
373 1980). In our dark perturbations, the primary production is halted altogether (the mass flux between
374 nutrients and phytoplankton is zero). The subsequent decline in population densities is going to be
375 mainly governed by the speed of mortality due to predation, and because at the reference state all rates
376 are slow, mortality by predation is slow as well. Thus, it will take longer for the ecosystem to reach the
377 “all dead” ultimate equilibrium, which means it is dynamically more resistant.

378 The resistance of a nutrient cycling system to a disturbance that alter population rates, like a climatic
379 perturbation, depends both in the ultimate displacement that would occur if the disturbance lasted in-
380 definitely and the rate at which the system approaches the ultimate displacement (Harrison and Fekete,
381 1980). This may be an issue when comparing the resistance to perturbations for different ecosystems. For
382 example, one ecosystem may have a slow approaching rate (high dynamical resistance) but with a very
383 large ultimate displacement. If the perturbation last long enough, this ecosystem may thus be classified
384 as less resistant than another ecosystem displaying fast approaching rates (low dynamical resistance) but
385 with a small ultimate displacement, even if dynamically the former is more resistant than later. Variations
386 in the ultimate displacement can partly explain the very complex behaviour of resistance with diversity
387 previously reported for a mass-conservative ecosystem (Loreau and Behera, 1999).

388 Our results, however, do not have such confounding effects. The dark-pulse perturbations ensures that
389 the ultimate displacement is fairly similar for all the ecosystems. For long enough periods of darkness, all
390 the mass in the system will be recovered in the dissolved inorganic nutrients pool. The euclidean distance
391 to this “all dead” system equilibrium state from the “all alive” unperturbed reference equilibrium state
392 (i.e. the ultimate displacement distance), although depending slightly on the particular position of the
393 reference equilibrium for each food web configuration, can be shown to be approximately the total mass
394 in the system for all of the food webs. Therefore, the resistance index we measure is a dynamical
395 resistance index; it is directly related to the speed at which the ecosystems approach the same ultimate
396 displacement.

397 The ecosystem resistance at the unperturbed reference equilibrium has been suggested to be related to the
398 resilience at the perturbed equilibrium (Harrison and Fekete, 1980). Furthermore, for very short ultimate
399 displacements, the unperturbed equilibrium and the perturbed equilibrium are so close that the ecosystem
400 dynamical resistance may be well characterized by its resilience at the unperturbed equilibrium alone. In
401 such case the dominant eigenvalue of Jacobian matrix at the unperturbed reference equilibrium gives the
402 dominant “response time” of the ecosystem to perturbations, and resilience and resistance can be seen
403 as opposite symmetric properties. Quick response times would imply high resilience and low resistance,
404 i.e. an ecosystem that will closely track climatic fluctuations (Harrison and Fekete, 1980).

405 However, for longer ultimate displacements like in our simulations, the information given by the Jaco-
406 bian matrix at the reference state may not serve to evaluate the ecosystem resistance at this point. In
407 these cases the dominant eigenvalue at the reference state cannot tell much about the speed of displace-
408 ment towards the ultimate displacement, because the unperturbed and perturbed equilibriums are so far
409 apart that they might well have very different resilience. Furthermore, even information about the local
410 resilience at the perturbed equilibrium might not be related to the resistance at the unperturbed reference
411 equilibrium because the Jacobian's linear approximation around the perturbed equilibrium is likely to
412 break down for long distances between these two points. Nevertheless, we tried to calculate the Jacobian
413 matrix at the "all dead" no-light perturbed equilibrium but we obtained an array of zeros for all food web
414 complexities. Therefore we were unable to relate the ecosystem resistance at the unperturbed reference
415 equilibrium to the ecosystem resilience at the perturbed equilibrium.

416 Yet, we find that information about the mass-cycling dynamical state of the reference equilibrium ex-
417 plains the observed variability in the resistance index. Our results show that the speed of displacement
418 towards the ultimate displacement is regulated by the rate of mass cycling through the food web at the
419 unperturbed equilibrium. Slow cycling of mass implies a high resistance to climatic disturbances. And
420 because the ecosystem is closed and in mass balance, total primary production alone gives a good mea-
421 sure of the average flux between compartments. This is the same to say that primary production gives a
422 measure of the mass turnover rate of the system at equilibrium. Thus, primary production might well be
423 used as a proxy of ecosystem resistance to climatic perturbations affecting population rates.

424 Recycling of nutrients has been argued to be a positive feedback (Webster et al., 1975). Less intense
425 nutrient recycling from predation losses (e.g. unassimilated mass) means that less nutrient is immediately
426 available for uptake by phytoplankton and thus instantaneous primary production is decreased (Loreau,
427 1996), which in turn slows down the whole cycling of mass through the system and therefore the mass
428 turnover rate. Our results show that reducing predation strength with food web complexity leads to a
429 slow nutrient recycling, slow primary production, slow mass turnover rate, and a high resistance. All this
430 while maximizing abiotic resource (nutrients) retention by the ecosystem as a whole, i.e. a high ratio of
431 total biotic to abiotic mass.

432 A reduction in predator-prey interactions with complexity has been suggested in the context of envi-
433 ronmental grain theory (Nunney, 1980). In coarse-grained environments (i.e. species tending to form
434 patches), predators must partition their search time between different prey species, lowering the func-
435 tional response of a predator to each of its prey (Nunney, 1980). However, whether or not higher number
436 of species in natural aquatic communities may lead to a decrease in the average predation strength still
437 remains speculative at this point, although this seems to be the case in terrestrial ecosystems (Montoya
438 et al., 2006). Nevertheless, the equations describing our aquatic food webs are analogues to those used
439 for terrestrial ecosystems (Fussmann and Heber, 2002). Therefore our results could be generalized to
440 any mass-conservative ecosystem, i.e. food webs for which primary production is mostly fuelled by the
441 recycling of nutrients within the system.

442 In any case, increasing prey chances of survival to predation with more species diversity seems a simple
443 mechanism by which an increase in food web complexity can lead to both an efficient nutrient retention
444 by the organisms in the food web and to a high resistance of the ecosystem itself to climatic fluctuations.
445 It should be stressed, however, that the dynamical mechanistic link is only between mass cycling rate
446 and resistance. The relationship between resistance and the average interaction strength just reflects that
447 the mass cycling rate can be affected by the level of predator-prey interactions; there is no dynamical
448 mechanistic link between resistance and the average interaction strength as such.

449 Furthermore, these results are not restricted to changes in predation efficiency with food web complexity.
450 The relationship between EAIS, primary production, mass turnover, and ecosystem resistance still holds
451 when we remove any influence of food web complexity and the only source of variability comes from the
452 randomly assigned parameter values (see Supp.Mat). This implies that any kind of source of variability
453 affecting the mass turnover rate in the ecosystem will affect the resistance of the food web. Thus, it
454 could be argued that ecosystems with slow primary production, regardless of its cause, should be more
455 resistant to climatic changes. Ongoing research is addressing this hypothesis by means of a global marine
456 ecosystem model where the number of plankton species is an emergent property (Follows et al., 2007;
457 Dutkiewicz et al., 2009; Barton et al., 2010).

458 Theoretical studies predict that community-level variability should increase with species richness, while
459 population-level variability should decrease (Ives et al., 2000; Cottingham et al., 2001). The stability
460 index we defined is based on the stationary distribution of the stochastic ecosystem (Ives et al., 2003).
461 Therefore, it gives a measure of population-level stability that characterize the system as a whole. Never-
462 theless, when we compared it to other measures of ecosystem variability such as the coefficient of varia-
463 tion at the population-level, community-level and the ecosystem-level, we obtain that all these measures
464 of stability give similar results. This implies that in our simulations there is no significant difference
465 between at which level (population, community, ecosystem) we evaluate the food web stability. That
466 means that a higher stability with food web complexity at the population-level causes a higher stability
467 at the community- and ecosystem-level as well.

468 What is more important for the overall stability of an ecosystem to climatic perturbations, its resilience or
469 its resistance? Our results suggest that resistance dominates. The variability of the food webs analyzed is
470 so buffered when they are resistant to climatic perturbations, that their resilience becomes unimportant.
471 In fact, the highest overall stability was found for the lowest resilient ecosystem. Furthermore, the
472 positive relationship between the resistance index and the overall stability index is almost as clear as
473 the one between mass turnover and resistance. There is no clear relationship between the resilience
474 index and the stability index but the trend is negative. We can then conclude that, regardless of their
475 resilience, persistent ecosystems with slow mass cycling through the food web are very stable thanks to
476 their increased resistance.

477 While our conclusions apply to perturbations of population rates (i.e. model parameters), they do not
478 necessarily apply to perturbations of population densities (i.e. model state-variables). The stability of an
479 ecosystem to inputs/outputs of its nutrients or organisms will not be related to the dynamical resistance
480 described here. For these type of perturbations resilience should dominate the overall stability of the
481 system. Also, the dynamical stability properties analyzed here are not related to structural stability
482 properties like robustness to species extinctions or vulnerability to species invasions. Being dynamically
483 stable to climatic disturbances does not necessarily mean being also structurally stable to species losses
484 or invasions.

485 **5 Conclusion**

486 We have analysed three dynamical stability properties of mass-conservative food web models: resilience,
487 resistance, and variability. The goal was to evaluate what determines the overall stability of complex
488 ecosystems to stochastic climatic perturbations affecting population rates. Although classical theory of
489 ecosystem resilience predicts that the stability of food webs should decrease with its complexity, our re-
490 sults demonstrate that this is not necessarily the case. We do find that resilience decreases with food web
491 complexity. However, resilience only measures the speed of recovery from fluctuations in pop-
492 ulation densities, it does not provide information about how difficult it may be to make the populations
493 fluctuate in the first place. This ecosystem sensitivity to climatic perturbations is given by the stability
494 property resistance. We find that if an increase of food web complexity is combined with a decrease in
495 the strength of predator-prey interactions, the overall stability of the ecosystem does in fact increase with
496 complexity. A lower average interaction strength causes a lower turnover rate of mass in the ecosystem,
497 and this increases its resistance to climatic perturbations. We evaluated the relative weight of resilience
498 and resistance on the overall stability of the food webs and show that resistance dominates. These results
499 suggest that more research should address the resistance of natural ecosystems to climatic perturbations,
500 since this stability property appears to be key for the overall stability of complex food webs and seems
501 to have been overlooked in previous theoretical studies.

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611 **Tables**

Term	Description	Equation	Units
E_{Z_j}	Excretion from zooplankton j	12	$\text{mmolN m}^{-3} \text{d}^{-1}$
E_C	Excretion from top carnivore fish	15	$\text{mmolN m}^{-3} \text{d}^{-1}$
F_{P_i}	Primary production of phytoplankton i	5	$\text{mmolN m}^{-3} \text{d}^{-1}$
F_{Z_j}	Secondary production of zooplankton j	11	$\text{mmolN m}^{-3} \text{d}^{-1}$
F_C	Secondary production of top carnivore fish	14	$\text{mmolN m}^{-3} \text{d}^{-1}$
$G_{P_i Z}$	Grazing on phytoplankton i from zooplankton	9	$\text{mmolN m}^{-3} \text{d}^{-1}$
$G_{Z_j Z}$	Predation on zooplankton j from zooplankton	9	$\text{mmolN m}^{-3} \text{d}^{-1}$
$G_{Z_j C}$	Predation on zooplankton j from top carnivore fish	13	$\text{mmolN m}^{-3} \text{d}^{-1}$
M_{P_i}	Natural mortality of phytoplankton i	16	$\text{mmolN m}^{-3} \text{d}^{-1}$
M_{Z_j}	Natural mortality of zooplankton j	17	$\text{mmolN m}^{-3} \text{d}^{-1}$
M_C	Natural mortality of top carnivore	18	$\text{mmolN m}^{-3} \text{d}^{-1}$

Table 1: List of model equations' terms

Parameter	Symbol	Value	Units
Phy. max. specific growth rate	μ_{P_i}	1.0*	d^{-1}
Phy. half-sat. for DIN uptake	k_{P_i}	0.1*	mmolN m^{-3}
Phy. natural mortality specific rate	m_P	0.05	d^{-1}
Phy. natural mortality density-dependence	γ_P	2.0	$\text{m}^3 \text{mmolN}^{-1}$
Zoo. max. specific ingestion rate	g_{Z_j}	1.0*	d^{-1}
Zoo. half-sat. const. for ingestion	k_{Z_j}	0.7*	mmolN m^{-3}
Zoo. predation efficiency const.	α	1/3	adim.
Zoo. assim. efficiency	β_Z	1/3	adim.
Zoo. natural mortality specific rate	m_Z	0.05	d^{-1}
Zoo. natural mortality density-dependence	γ_Z	2.0	$\text{m}^3 \text{mmolN}^{-1}$
Fish max. specific ingestion rate	g_C	1.0	d^{-1}
Fish half-sat. const. for ingestion	k_C	1.0	mmolN m^{-3}
Fish assim. efficiency	β_C	1/3	adim.
Fish natural mortality rate	m_C	0.2	d^{-1}
Fish natural mortality density-dependence	γ_C	2.0	$\text{m}^3 \text{mmolN}^{-1}$
Fish carrying capacity	K_C	0.5	mmolN m^{-3}

Table 2: List of model parameters.

* Mean value μ from a Gaussian distribution with standard deviation $\sigma = 0.2 \mu$

612 **Figures**Figure legends

- 613 • Fig. 1 Topology diagrams for the 12 food web complexities. Note that only predator-prey interac-
 614 tions are shown (i.e. nutrients and recycling arrows are not included for simplicity). Color nodes
 615 represent food web plankton functional types (PFT): green for phytoplankton (small, medium,
 616 large; from left to right); blue for micro-zooplankton; black for meso-zooplankton; yellow for
 617 macro-zooplankton; red for mega-zooplankton; and gray for top carnivore fish. The size of the
 618 nodes indicates the size of the PFT (not true scale). The color of the lines indicate predation on
 619 a given prey, except for gray dashed lines which represent predation by top predator fish on all
 620 zooplankton (closure term).
- 621 • Fig. 2 Steady state concentrations under no light-limited conditions as a function of phytoplank-
 622 ton complexity (**p-cmpx**) and zooplankton complexity (**z-cmpx**): a) total phytoplankton; b) total
 623 zooplankton; c) top carnivore fish; d) dissolved inorganic nutrients. Units [mmolN m^{-3}].
- 624 • Fig. 3 Steady state flux rates under no light-limited conditions as a function of phytoplankton
 625 complexity (**p-cmpx**) and zooplankton complexity (**z-cmpx**): a) total phytoplankton production;
 626 b) total zooplankton production; c) total top carnivore fish production; d) recycling production of
 627 dissolved inorganic nutrients. Units [$\text{mmolN m}^{-3} \text{d}^{-1}$].
- 628 • Fig. 4 Ecosystem interaction strength and stability indices as a function of phytoplankton com-
 629 plexity (**p-cmpx**) and zooplankton complexity (**z-cmpx**): a) average interaction strength of the
 630 Interaction matrix [$\text{m}^3 \text{mmolN}^{-1} \text{d}^{-1}$]; b) resilience index (99.99% recovery rate for the sin-
 631 gular perturbation, [d^{-1}]); c) resistance index (perturbation time for the single perturbation, [d]);
 632 d) stability index (inverse of the φ parameter of the Weibull distribution of the distances to the
 633 steady-state for the stochastic perturbation, $1 / [\text{mmolN m}^{-3}]$).
- 634 • Fig. 5 Probability distribution functions (PDF) of the distances to the reference steady-state point

635 (SSP) for the stochastic perturbation as a function of phytoplankton complexity (**p-cmpx**) and
 636 zooplankton complexity (**z-cmpx**). The gray dots are the observed distances to the steady-state (n
 637 = 365) and the black-line is the stationary Weibull distribution that fits the raw data.

638 • Fig. 6 Dynamics of the stochastic ecosystems: a) trajectories in the phase plane for the least
 639 (blue lines) and most complex (black lines) food web. The red dot gives the steady-state. The
 640 yellow dots gives the mean position of the trajectories. The concentration of total phytoplankton,
 641 total zooplankton and dissolved inorganic nutrients have been centered by subtracting the steady-
 642 state value: $x(t) = X(t) - X^*$; b) time-series, for the least (upper panel) and most complex
 643 (lower panel) food web, of total phytoplankton (green continuous line), total zooplankton (blue
 644 continuous line), and dissolved inorganic nutrients (yellow continuous line). The dotted lines give
 645 their steady-state concentration. Random days in which solar radiation is zero are shown as gray
 646 vertical bars. Units [mmolN m^{-3}].

647 • Fig. 7 Relationship between the dominant eigenvalue of the Jacobian matrix and: a) average
 648 interaction strength between species computed from the elements in the Interaction matrix [m^3
 649 $\text{mmolN}^{-1} \text{d}^{-1}$]; b) inverse of the resistance index (perturbation rate [d^{-1}]); c) inverse of the
 650 stability index (φ parameter of the Weibull distribution for the distances to the steady-state in the
 651 stochastic perturbation [mmolN m^{-3}]); d) return rate [d^{-1}] (dimensionless values obtained by
 652 normalizing by the mean).

653 • Fig. 8 Relationship between total primary production and: a) inverse of the resistance index (per-
 654 turbation rate [d^{-1}]); b) average interaction strength between species computed from the elements
 655 in the Interaction matrix [$\text{m}^3 \text{mmolN}^{-1} \text{d}^{-1}$]; c) inverse of the stability index (φ parameter of
 656 the Weibull distribution for the distances to the steady-state in the stochastic perturbation [mmolN
 657 m^{-3}]); d) average flux rate (primary production not included) of mass cycling through the food
 658 web [$\text{mmolN m}^{-3} \text{d}^{-1}$] (dimensionless values obtained by normalizing by the mean).

659 • Fig. 9 Relationship between the inverse of the stability index and: a) coefficient of variation for

660 the concentration of individual populations (i.e. individual phytoplankton and individual zooplank-
661 ton); b) coefficient of variation for the concentration of functional communities (i.e. aggregated
662 phytoplankton and aggregated zooplankton); c) coefficient of variation for the average flux rate
663 (primary production not included) of mass cycling through the food web; d) inverse of the stabil-
664 ity index using the raw data (i.e. without fitting a Weibull distribution). (Dimensionless values
665 obtained by normalizing by the mean)

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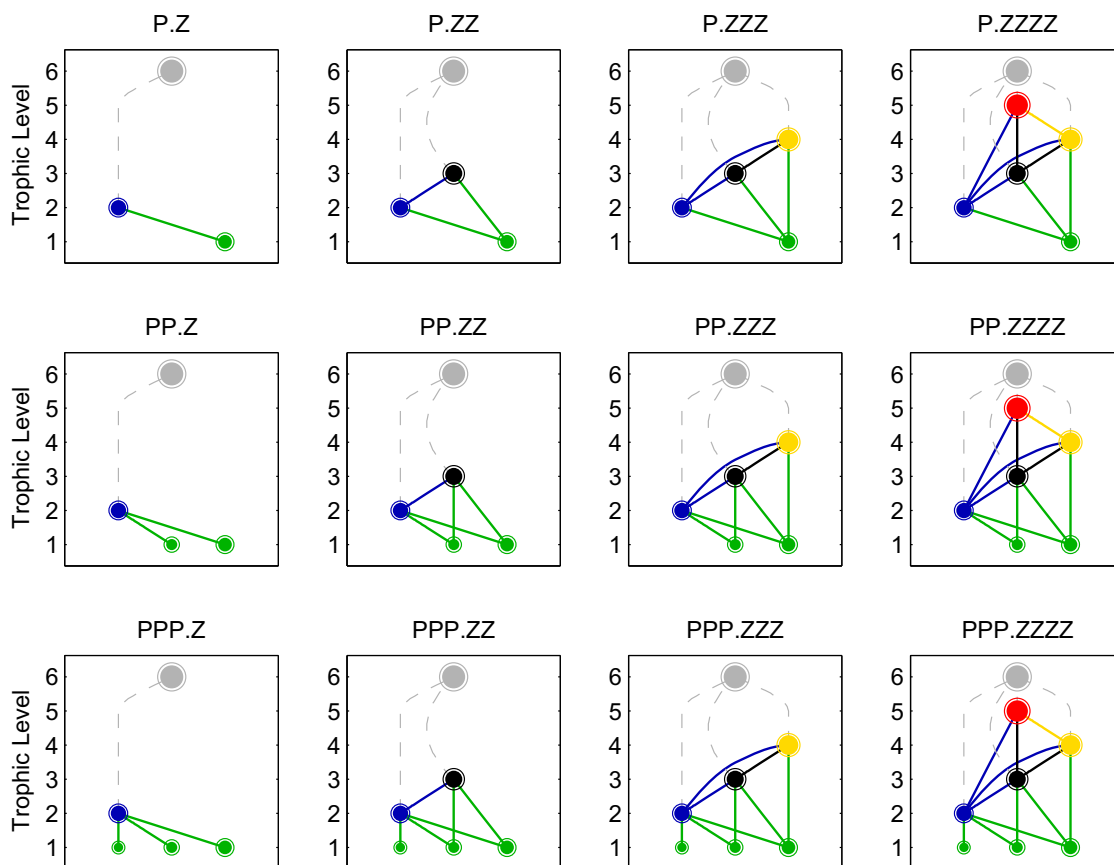


Figure 1

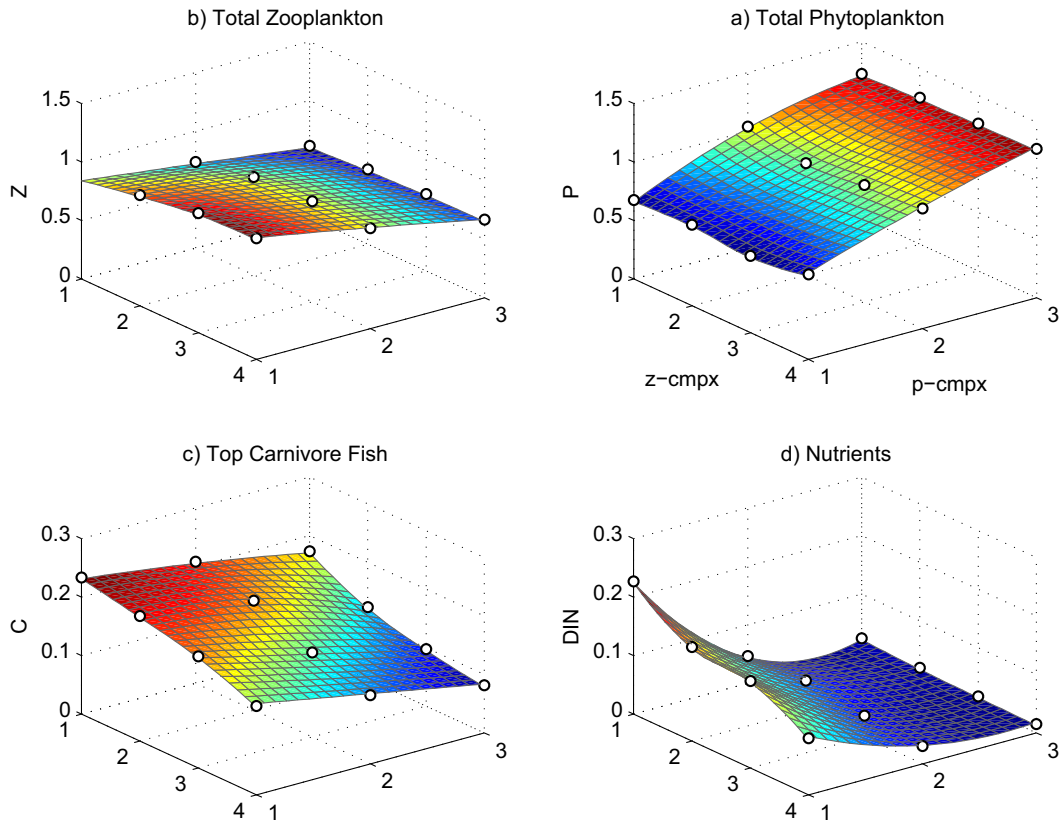


Figure 2

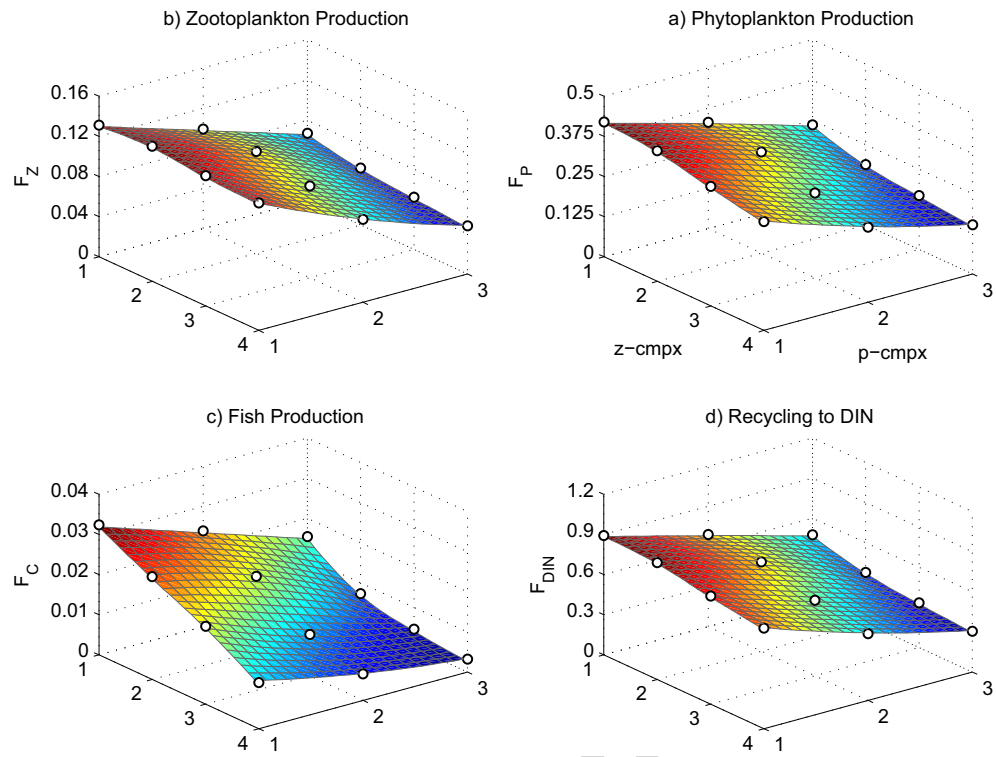


Figure 3

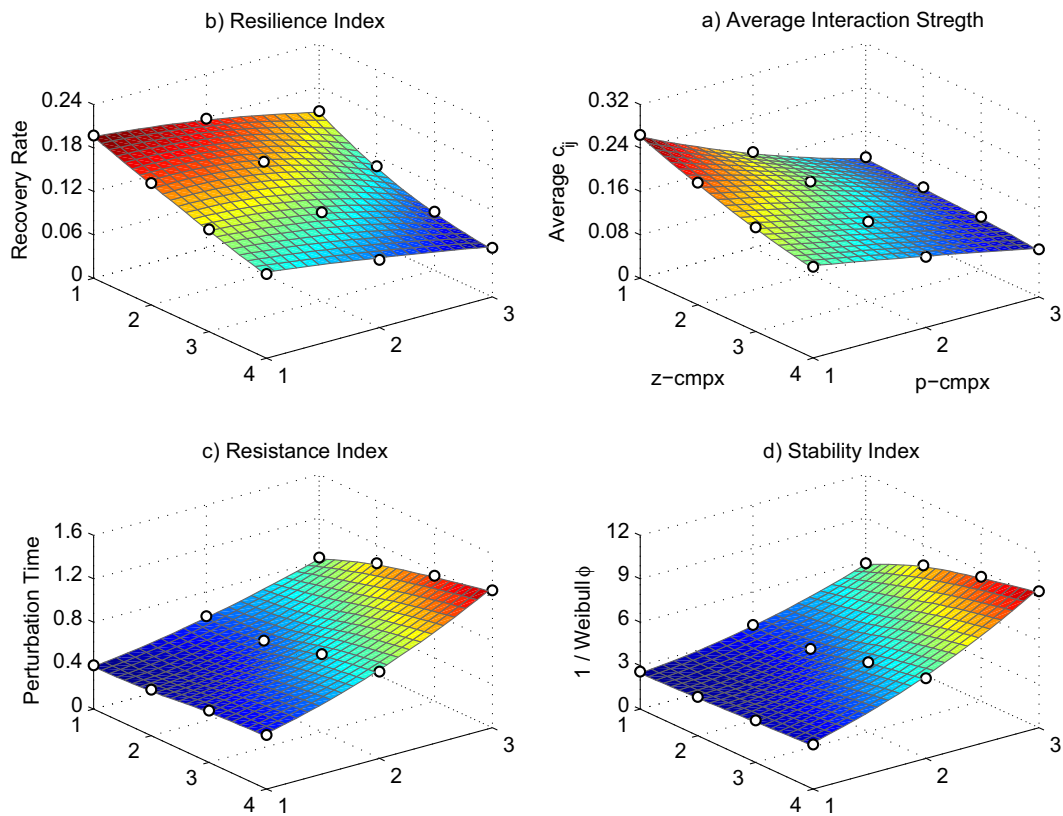


Figure 4

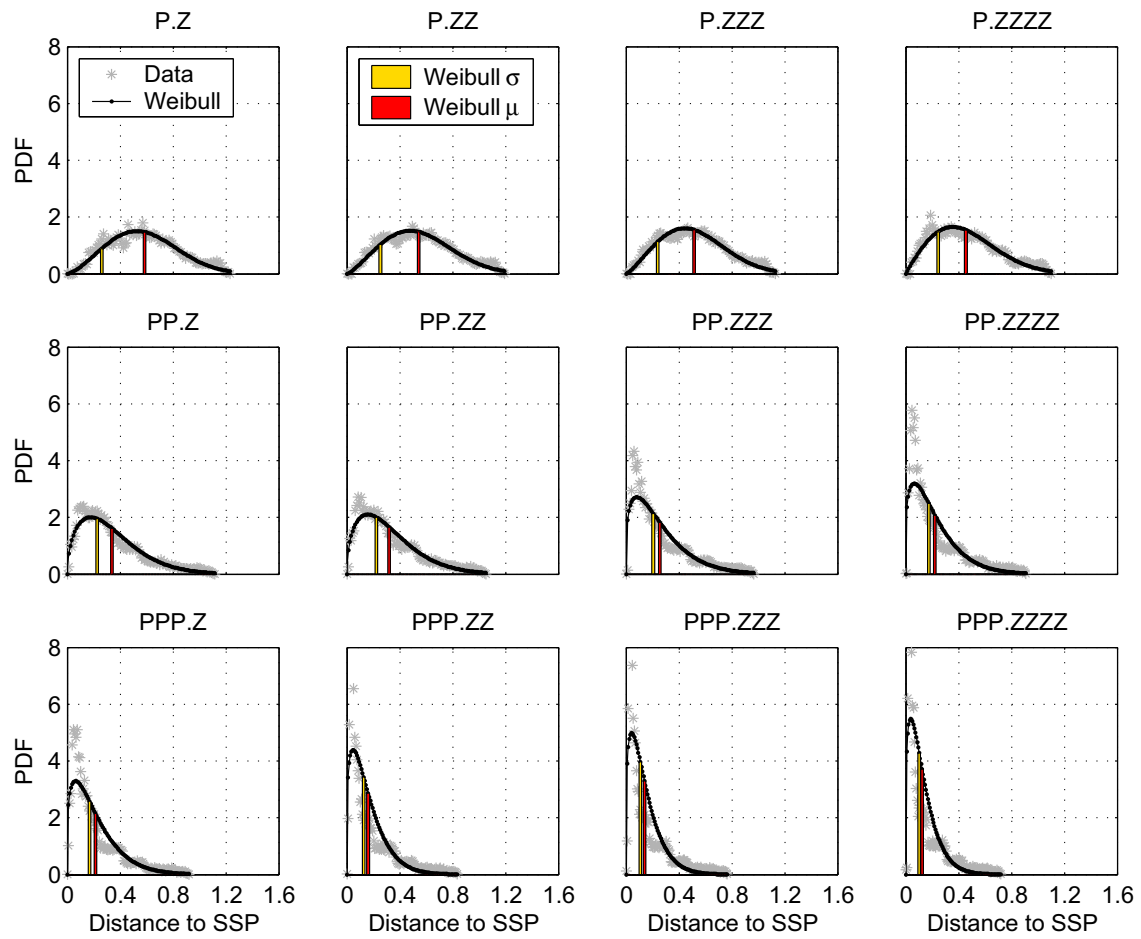


Figure 5

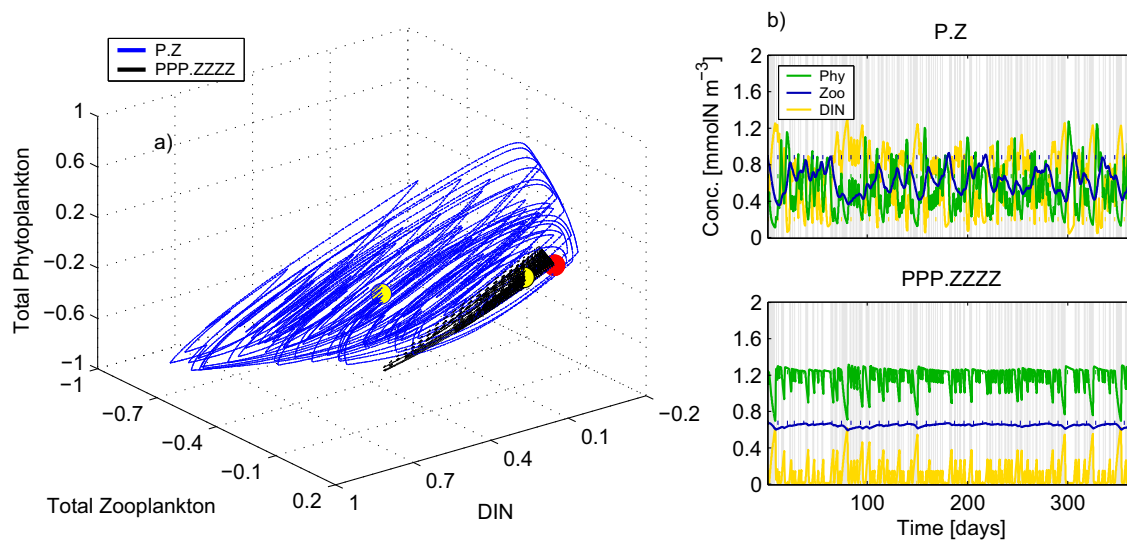


Figure 6

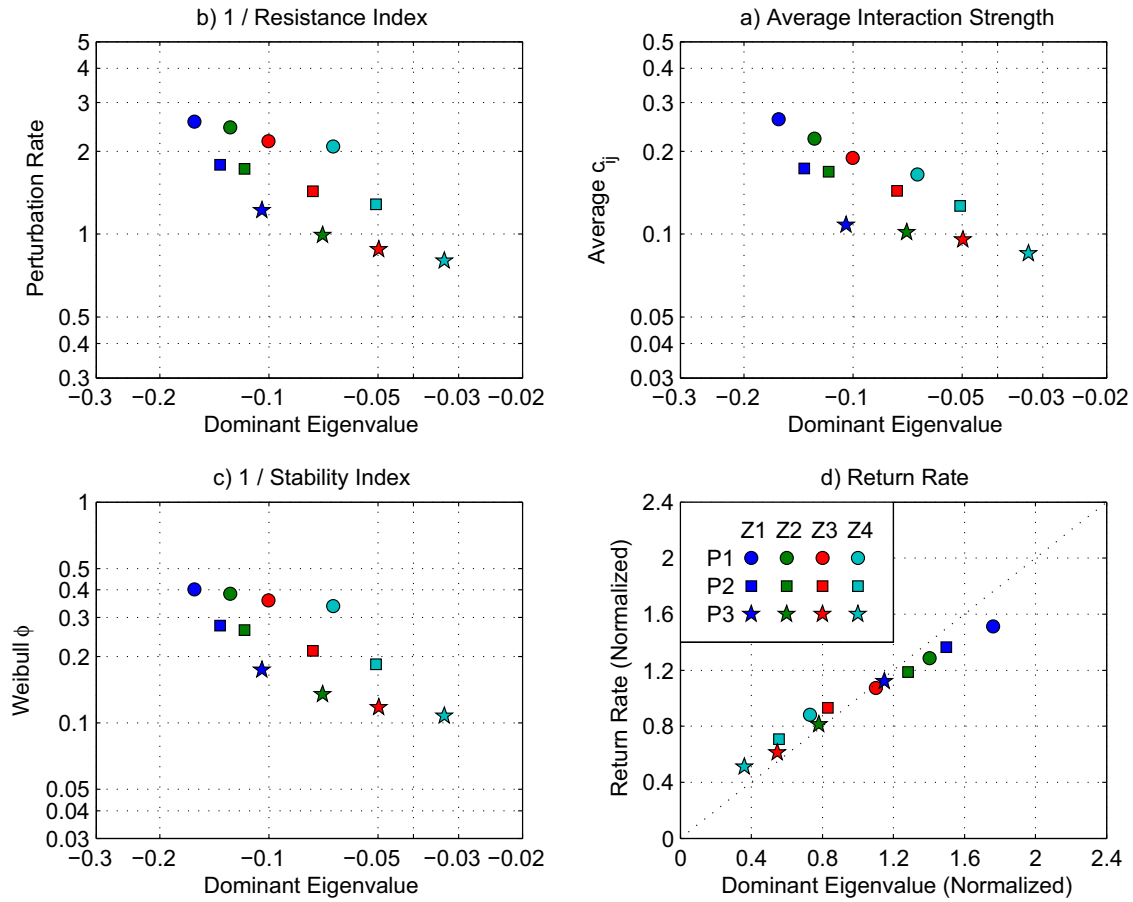


Figure 7

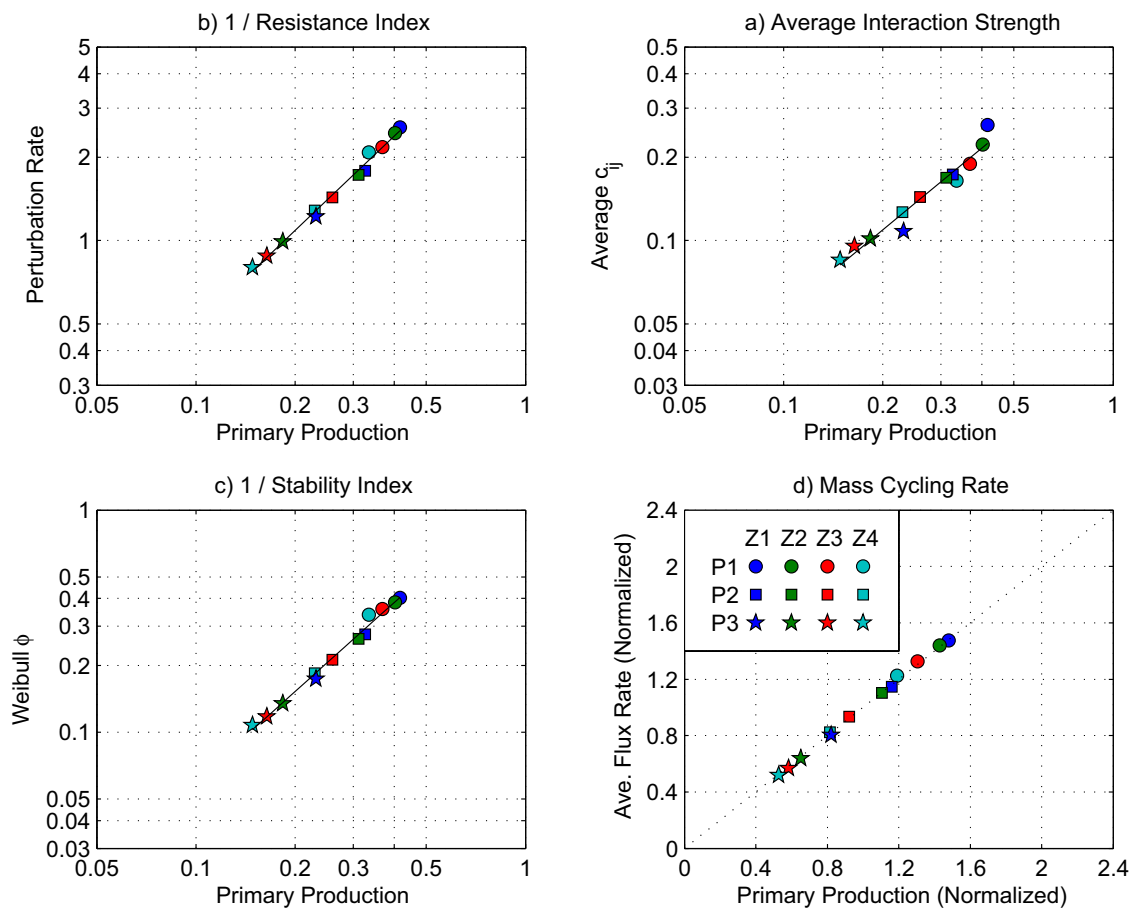


Figure 8

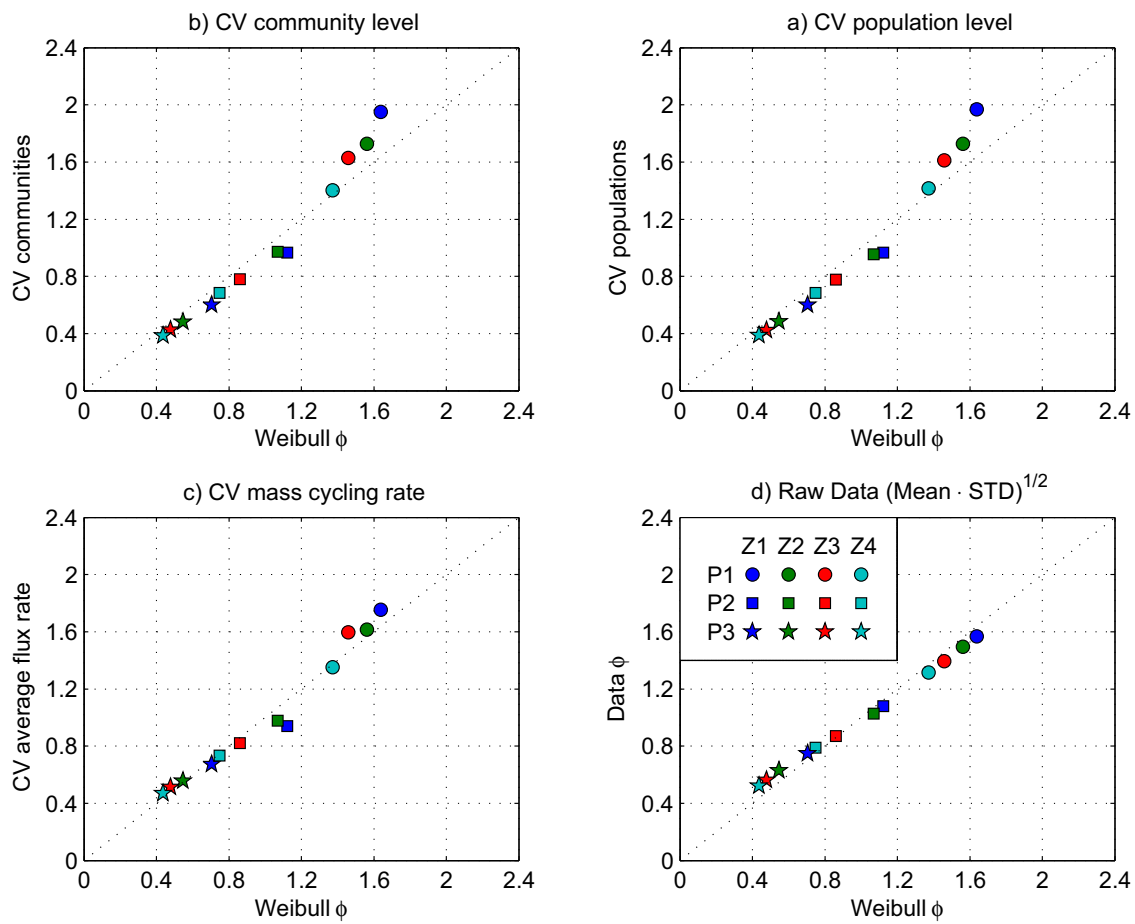


Figure 9