



MODELING BIODIVERSITY IN THE CONTEXT OF COMPETITION BETWEEN TWO INTERACTING PHYTOPLANKTON SPECIES

*IGWE P.Y; **OLOWU B.J AND ***EKAKA-A E.N

, federal College of Education (Technical) Omoku, Rivers State. *** department of Mathematics, Rivers State University, Port Harcourt, Nigeria*

ABSTRACT

Modeling the effect of decreasing the inter-competition coefficient between two phytoplankton species from the value of 0.0025 to 0.0125 has clearly shown an evidence of biodiversity gain for the first phytoplankton species and a biodiversity loss for the second phytoplankton species. Therefore, an appropriate ecological policy should be put in place to sustain the biodiversity gain and also to mitigate against the loss of biodiversity. These novel results obtained in this paper has not been seen elsewhere, they are presented and discussed.

INTRODUCTION

The quality of a marine environment depends on the quality and quantity of most aquatic organisms. One of those organisms is the phytoplankton species. Phytoplankton is a Greek word, where “Phyton” means plant and ‘plantos’ means wanderer or drifter. They lack the ability to move and as such depend on the current of the river or ocean for locomotion. They are usually found mainly where there is water and sunlight.

Phytoplankton are singled –celled organism of lakes, streams, and oceans. They are often tiny in size and could not be seen with the ordinary eyes in most case. Regardless of their size, they have great impact on the Ecosystem. They play an important role in photosynthesis as they convert sunlight in to the chemical energy that powers life on earth. Phytoplankton just like terrestrial plants release oxygen into the atmosphere and so produce about a high proportion of the worlds oxygen. There are various kinds of phytoplankton, they are; cyanobacteria (also referred to as blue – green algae or the blue –green bacteria),

silica – encased diatoms, *dinoflagellates*, green algae and chalk – coated *coccolithophores*. However, diatoms and dinoflagellates are the most common kinds of phytoplankton. (Abbas *et al.*, (2010), Albrecht *et al.*, (1974), Addicott (1981), Baker and Buckwar (2000), Balvanera *et al.*, (2006), Bandyopadhyay (2006), Bandyopadhyay *et al.*, (2008), Cardinale *et al.*, (2012), Cardinale *et al.*, (2006), Chattopadhyay *et al.*, (2002), Clapham (1973), Ekaka-a (2009), Fisher *et al.*, (2009), Hernández-Bermejo and Fairén (1995), Hooper et al (2005), Jasprica and Car (2003), Ji, *et al.*, (2009), Jiang *et al.*, (2012), Levis (1979), Liu, and Lou (2010), Loreau and Wardle (2001), Marine Biology Organization (MBO), (2007), May (1973), Melian *et al.*, (2008). Pal (2005), Pal *et al.*, (2008), Liu, and Lou (2010), Duggins (1981), Rehim and Mudassor (2010), Rice (1984), Rice (1987), Sarkar and Chattopadhyay (2003), Sinha *et al.*, (2009), Solé, *et al.*, (2005). Tapaswi and Mukhopadhyay, (1999). Tilman (1996). Townsend *et al.*, (2009). Wallace, (2007), Wokoma, and Friday (2016). Worm et al.,(2006), Yachi, and Loreau (1999)).

The study of phytoplankton has span over the years because of its relative importance which include:

- (1) They are primary producers that is to say they are the foundation of the aquatic food web as they are serve as food for aquatic creatures as well as humans. (Wokoma and Friday, 2009)
- (2) They serve as bio-monitoring of pollution (Davis et al., 2009)
- (3) The biological integrity of the water body could be assessed by the distribution, abundance and composition of the phytoplankton species (Townsend et al., 2009)
- (4) They reflect the nutrient status of the marine environment (Marine Biology organization (MBO).
- (5) Phytoplankton could be eaten as food (bigger species), also used for the production of nutritional supplement and serve as fertilizers.

MATERIALS AND METHOD

We have considered the following Lotka–Volterra model equations of competition indexed by a system of continuous non-linear first order ordinary differential equations (Bandyopadhyay, Saha, Pal, (2008)):

$$\frac{dN_1(t)}{dt} = N_1(t)[\alpha_1 - \beta_1 N_1(t) - \gamma_1 N_2(t)] \quad 1$$

$$\frac{dN_2(t)}{dt} = N_2(t)[\alpha_2 - \beta_2 N_2(t) - \gamma_2 N_1(t)] \quad 2$$

Here, the initial conditions are defined by $N_1(0) = N_{10} \geq 0$ and $N_2(0) = N_{20} \geq 0$, whereas $N_1(t)$ and $N_2(t)$ specify the densities of the two phytoplankton species (measured as the number of cells per liter). For the purpose of this formulation, α_1 and α_2 specify the cell proliferation rate per day; β_1 and β_2 specify the rate of intra-specific competition terms for the first and second species; γ_1 and γ_2 specify the rate of inter-specific competition. The units of $\alpha_1, \alpha_2, \beta_1, \beta_2, \gamma_1$ and γ_2 are per day per cell and day is the unit of time. We have defined the parameter values as proposed by Bandyopadhyay, Saha, Pal, (2008), as $\alpha_1 = 2, \alpha_2 = 1, \beta_1 = 0.07, \beta_2 = 0.08, \gamma_1 = 0.05, \gamma_2 = 0.015$.

We shall state the method used with the following under listed steps.

Step 1: Consider a scenario where $N_1(\text{old})$ is the predicted biomass [$N_1(\text{old})$ is the population density of the first phytoplankton species otherwise called the biomass of the first phytoplankton species when all other parameter values are fixed at time t.

Step 2: Replace $N_1(\text{old})$ with $N_1(\text{new})$ due to a variation of the inter-competition coefficient γ_1 .

Step 3: If $N_1(\text{new})$ is strictly less than $N_1(\text{old})$, it indicates that the variation of γ_1 has predicted a depletion which mimics biodiversity loss. In this scenario, the appropriate mathematically formula for the quantification of biodiversity loss is defined as follows:

$$\text{BL (\%)} = 100 \left[\frac{N_1(\text{old}) - N_1(\text{new})}{N_1(\text{old})} \right]$$

Step 4: If $N_1(\text{new})$ is strictly greater than $N_1(\text{old})$, due to the variation of γ_1 , then a biodiversity gain has occurred which can be similarly defined as follows:

$$\text{BG (\%)} = 100 \left[\frac{N_1(\text{new})}{N_1(\text{old})} - 1 \right]$$

Step 5: Consider a scenario where $N_1(\text{old})$ is the predicted biomass [$N_1(\text{old})$ is the population density of the first phytoplankton species otherwise called the biomass of the first phytoplankton species when all other parameter values are fixed at time t.

Step 6: Replace $N_2(\text{old})$ with $N_2(\text{new})$ due to a variation of the inter-competition coefficient γ_2 .

Step 7: If $N_2(\text{new})$ is strictly less than $N_2(\text{old})$, it indicates that the variation of γ_2 has predicted a depletion which mimics biodiversity loss. In this scenario, the

appropriate mathematical formula for the quantification of biodiversity loss is defined as follows:

$$BL (\%)=100\left[\frac{N_1(old)-N_1(new)}{N_1(old)}\right]$$

Step 8: If $N_2(new)$ is strictly greater than $N_2(old)$, due to the variation of γ_2 , then a biodiversity gain has occurred which can be similarly defined as follows:

$$BG (\%)=100\left[\frac{N_1(new)}{N_1(old)} - 1\right]$$

RESULTS

On the application of the above methods, we have obtained the following empirical results;

Table 1: Evaluating the extent of biodiversity for $\gamma_1 = 0.0025$ with experimental time of 10 years using MATLAB ODE 45 numerical scheme

Years	N_1	N_{1m}	BG(%)	N_2	N_{2m}	BL (%)
1	4.0000	4.0000	0.00	10.0000	10.0000	0.00
2	10.6819	15.3277	43.49	10.6094	10.3688	2.27
3	17.3033	25.2777	46.09	10.1236	9.3174	7.96
4	20.5151	27.8109	35.56	9.4452	8.3657	11.43
5	21.7063	28.2210	30.01	8.9593	7.8268	12.64
6	22.1823	28.2877	27.52	8.6637	7.5394	12.98
7	22.4060	28.3033	26.32	8.4908	7.3843	13.03
8	22.5238	28.3089	25.68	8.3900	7.2991	13.00
9	22.5896	28.3115	25.33	8.3312	7.2518	12.96
10	22.6273	28.3129	25.13	8.2967	7.2253	12.91

N_1 : Controlled data sets for the first phytoplankton species

N_{1m} : Perturbed data sets for the first phytoplankton species

BG(%): Biodiversity gain in percentage

N_2 : Controlled data sets for the second phytoplankton species

N_{2m} : Perturbed data sets for the second phytoplankton species

BL(%): Biodiversity loss in percentage

Table 2: Evaluating the extent of biodiversity for $\gamma_1 = 0.005$ with experimental time of 10 years using MATLAB O.D.E 45 numerical scheme

Years	N_1	N_{1m}	BG(%)	N_2	N_{2m}	BL (%)
1	4.0000	4.0000	0.00	10.0000	10.0000	0.00
2	10.6819	15.0537	40.93	10.6094	10.3827	2.14
3	17.3033	24.8670	43.71	10.1236	9.3609	7.53
4	20.5151	27.4698	33.90	9.4452	8.4187	10.87
5	21.7063	27.9235	28.64	8.9593	7.8802	12.05
6	22.1823	28.0085	26.27	8.6637	7.5915	12.38
7	22.4060	28.0328	25.11	8.4908	7.4353	12.43
8	22.5238	28.0429	24.50	8.3900	7.3493	12.40
9	22.5896	28.0480	24.16	8.3312	7.3015	12.36
10	22.6273	28.0508	23.97	8.2967	7.2746	12.32

N_1 : Controlled data sets for the first phytoplankton species

N_{1m} : Perturbed data sets for the first phytoplankton species

BG(%): Biodiversity gain in percentage

N_2 : Controlled data sets for the second phytoplankton species

N_{2m} : Perturbed data sets for the second phytoplankton species

BL(%): Biodiversity loss in percentage

Table 3:Evaluating the extent of biodiversity for $\gamma_1 = 0.0075$ with experimental time of 10 years using MATLAB ODE 45 numerical scheme

Years	N_1	N_{1m}	BG(%)	N_2	N_{2m}	BL (%)
1	4.0000	4.0000	0.00	10.0000	10.0000	0.00
2	10.6819	14.7829	38.39	10.6094	10.3965	2.01
3	17.3033	24.4543	41.33	10.1236	9.4044	7.10
4	20.5151	27.1239	32.21	9.4452	8.4722	10.30
5	21.7063	27.6213	27.25	8.9593	7.9342	11.44
6	22.1823	27.7251	24.99	8.6637	7.6443	11.77
7	22.4060	27.7584	23.89	8.4908	7.4870	11.82
8	22.5238	27.7732	23.31	8.3900	7.4002	11.80
9	22.5896	27.7809	22.98	8.3312	7.3519	11.76
10	22.6273	27.7851	22.80	8.2967	7.3247	11.72

N_1 : Controlled data sets for the first phytoplankton species

N_{1m} : Perturbed data sets for the first phytoplankton species

BG(%): Biodiversity gain in percentage

N_2 : Controlled data sets for the second phytoplankton species

N_{2m} : Perturbed data sets for the second phytoplankton species

BL(%): Biodiversity loss in percentage

Table 4: Evaluating the extent of biodiversity for $\gamma_1 = 0.01$ with experimental time of 10 years using MATLAB ODE 45 numerical scheme

Years	N_1	N_{1m}	BG(%)	N_2	N_{2m}	BL (%)
1	4.0000	4.0000	0.00	10.0000	10.0000	0.00
2	10.6819	14.5154	35.89	10.6094	10.4102	1.88
3	17.3033	24.0396	38.93	10.1236	9.4478	6.68
4	20.5151	26.7732	30.51	9.4452	8.5261	9.73
5	21.7063	27.3143	25.84	8.9593	7.9888	10.83
6	22.1823	27.4376	23.69	8.6637	7.6978	11.15
7	22.4060	27.4800	22.65	8.4908	7.5394	11.21
8	22.5238	27.4997	22.09	8.3900	7.4519	11.18
9	22.5896	27.5100	21.78	8.3312	7.4030	11.14
10	22.6273	27.5156	21.60	8.2967	7.3754	11.10

N_1 : Controlled data sets for the first phytoplankton species

N_{1m} : Perturbed data sets for the first phytoplankton species

BG(%): Biodiversity gain in percentage

N_2 : Controlled data sets for the second phytoplankton species

N_{2m} : Perturbed data sets for the second phytoplankton species

BL(%): Biodiversity loss in percentage

Table 5: Evaluating the extent of biodiversity for $\gamma_1 = 0.0125$ with experimental time of 10 years using MATLAB ODE 45 numerical scheme

Years	N_1	N_{1m}	BG(%)	N_2	N_{2m}	BL (%)
1	4.0000	4.0000	0.00	10.0000	10.0000	0.00
2	10.6819	14.2512	33.41	10.6094	10.4237	1.75
3	17.3033	23.6231	36.52	10.1236	9.4912	6.25
4	20.5151	26.4177	28.77	9.4452	8.5805	9.16
5	21.7063	27.0024	24.40	8.9593	8.0441	10.22
6	22.1823	27.1456	22.38	8.6637	7.7520	10.52
7	22.4060	27.1976	21.39	8.4908	7.5926	10.58
8	22.5238	27.2222	20.86	8.3900	7.5042	10.56
9	22.5896	27.2352	20.57	8.3312	7.4548	10.52

10	22.6273	27.2424	20.40	8.2967	7.4269	10.48
-----------	---------	---------	-------	--------	--------	-------

N_1 : Controlled data sets for the first phytoplankton species

N_{1m} : Perturbed data sets for the first phytoplankton species

BG(%): Biodiversity gain in percentage

N_2 : Controlled data sets for the second phytoplankton species

N_{2m} : Perturbed data sets for the second phytoplankton species

BL(%): Biodiversity loss in percentage

DISCUSSIONS

What can we deduce from the result presented in tables 1 to 5? By decreasing the contribution of the second phytoplankton species on the first phytoplankton species which was denoted by γ_1 , from the value of 0.0025 to 0.0125, the biodiversity loss effect due to the initial condition remains at the value of 0. We have also observed that each volume of biodiversity gain is decreasing irrespective of the decreasing value of γ_1 . It is worth mentioning that the biodiversity volume of 43.49% for the second year when $\gamma_1 = 0.0025$ (Table 1) decreases to 40.93% when $\gamma_1 = 0.005$ (Table 2), it also decreases to 38.39% when the value of $\gamma_1 = 0.0075$ (Table 3), it continues to decrease to 35.85% when the value of $\gamma_1 = 0.01$ (Table 4) and in this context decreases to 33.41% when $\gamma_1 = 0.0125$ (Table 5).

Over a ten year numerical simulation we have observed that the volume of biodiversity gain when $\gamma_1 = 0.0025$ (Table 1) is 25.13%. This observed volume of biodiversity gain decreases to 23.97% for $\gamma_1 = 0.05$ (Table 2), to 22.80% for $\gamma_1 = 0.0075$ (Table 3) to 21.00% for $\gamma_1 = 0.01$ (Table 4) and to 20.40% for $\gamma_1 = 0.0125$ (Table 5).

On the basis of these prediction of biodiversity gain, we clearly see that the changes in the γ_1 parameter value which in this context is an indication of a decreasing pattern of the original value of γ_1 dominantly predicts biodiversity gain which is decreasing in volume. The ecological implication of this numerical simulation predictions is that when the contribution of the second phytoplankton species to inhibit the growth of the first phytoplankton species is weakened the biodiversity value response is dominantly a gain which has shown a decrease for the following changing values of γ_1 : $\gamma_1 = 0.0025, 0.005, 0.0075, 0.01$ and 0.0125 .

RECOMMENDATIONS

We can apply the same numerical methods which we have used to answer the following unsolved questions.

- i) What is the effect of varying the intra-competition coefficients of the two competing Phytoplankton species on the biodiversity?
- ii) What is the effect of varying the initial conditions on the biodiversity?

CONCLUSION

We have successfully applied the method of ODE 45 that is indexed by a MATLAB programming function to obtain instances of the biodiversity gain with respect to the first Phytoplankton species and instances of biodiversity loss with respect to the second Phytoplankton species due to a decrease variation of the inter-competition coefficient which in this context is defined as the contributions of the second Phytoplankton species to inhibit the growth of the first Phytoplankton species. In particular, the first phytoplankton species is predicted to benefit from a biodiversity gain which involves some sort of Ecological services sustainability provided the inter-competition coefficient ranges from 0.0025 to 0.0125 whereas the same range of values of the inter-competition coefficients has predicted a biodiversity loss for the second Phytoplankton species which has implication for the loss of Ecological services. On both biodiversity scenarios relevant policies should be put into place to sustain the predicted biodiversity gain and to mitigate against the loss of biodiversity. All the same, adequate funding is needed in which a sophisticated numerical method can be used to find a region of transition from biodiversity gain to a biodiversity loss for the first phytoplankton species and a transition from a biodiversity loss to a biodiversity gain for the second phytoplankton species. We would expect these further contribution subject to the availability of funding to provide more insight on the sustainability of ecosystem functioning which we did not do in this present study.

REFERENCES

- Abbas, S., Banerjee M, & Hungerbuhlar N., (2010). Existence, uniqueness and stability of allelopathic stimulatory phytoplankton model. *Journal of Mathematical Analysis and Application.* doi:10.1016/j.jmaa2010.01.024

- Albrecht, F., Gatzke, H., Hadad, A & Wax N., (1974). The dynamics of two interacting populations. *Journal of Mathematical Analysis and Application.* 46(3):658-670.
- Addicott, J.F (1981). Stability Properties of 2-species models of mutualism: Simulation studies. *Oecologia.* 49(1):42-49.
- Baker, CTH., & Buckwar E., (2000). Numerical Analysis of explicit one-step methods for stochastic Delay differential equations. *LMS Journal of Computational Mathematics.* 3: 315-335.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology letters.* 9:1146-1156.
- Bandyopadhyay M. (2006). Dynamical analysis of allelopathic phytoplankton model. *Journal of Biological System.* 14: 205–218.
- Bandyopadhyay, M., Saha, T., & Pal, R. (2008). Deterministic and Stochastic analysis of a delayed allelopathic phytoplankton model within fluctuating environment, Elsevier. 2:958–970.
- Cardinale, B. J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., & Naeem, S. (2012). Biodiversity loss and its impact on humanity, *Nature.*486: 59-67.
- Cardinale, B.J., Srivastava, D.S., Duffy, J.E, Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *International Journal of Science. (Nature).*443:989–992.
- Chattopadhyay, J., Sarkar, R.R., & Mondal, S. (2002). Toxin-producing phytoplankton may act as a biological control for planktonic blooms-field study and mathematical modeling. *Journal of Theoretical Biology.* 215: 333–344.
- Clapham CRJ. (1973).In: Introduction to mathematical analysis.
- Davies, O.A., Tawari, C.C. & Abowei, J.F.N., (2009). Zooplankton of Elechi Creek, Niger Delta Nigeria. *Environmental Ecology.* 26(4c): 2441-2346.
- Ekaka-a, E.N. (2009). Computational and mathematical modelling of plant species interactions in a harsh climate. Ph.D Thesis, Department of Mathematics. The University of Liverpool and The University of Chester, United Kingdom.
- Fisher, B.R., Turner, K., & Morling, P. (2009). Defining and classifying ecosystem services for decision making. Elsevier 68(3):643-653.
- Hernández-Bermejo, B., & Fairén, V., (1995). Lotka-Volterra representation of general nonlinear systems. *Mathematical Bioscience.* 140: 1–32.
- Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., ... & Wardle, D. A. (2005). Effects of Biodiversity on Ecosystem functioning: A consensus of current knowledge. *DOI:10.1890104-0922.*
<http://en.m.wikipedia.org>
- Jasprica, N. & Car, A. (2003). Toxic and potentially toxic phytoplankton species. “*Nase more*”. 50(1-2): 68-71.
- Ji, C., Jiang, D., & Shi, N. (2009). Analysis of a predator prey model with modified Leslie Gower and Holling-type II schemes with stochastic perturbation. *Journal of Mathematical Analysis and Application.* 359(2): 482-498.
- Jiang, D., Ji, C., Li, X., & O’Regan, D. (2012). Analysis of autonomous Lotka- Volterra competition systems with random perturbation. *Journal of Mathematical Analysis and Application.* 390:582-595.
- Levis, R. (1979). Co-existence in a variable environment. *The American Naturalist.* 114(6).

- Liu, X., & Lou, Y. (2010). Global dynamics of a predator-prey model. *Journal of Mathematical Analysis and Application*. 371:323-340.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, P., Hector, A., & Wardle, D.A., (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*. 294(5543):804-808.
- Marine Biology Organization (MBO), (2007). *Zooplankton*. Retrieved September 29, 2006 from <http://www.marinebio.com/oceans/zooplanktons>. Asp-62k
- May, R.M., (1973). Qualitative Stability in Model Ecosystems, DOI:10.2307/19353552.
- Melian, C.J., Bascompte, J., Jordano, P., & Krivan V (2008). Diversity in a complex ecological network with two interaction types. DOI:10.1111/j.1600.0706.2008.16751.x
- Pal, S. (2005). Role of toxin producing phytoplankton for coexistence of planktonic ecosystem. Workshop on quantitative ecology.
- Pal, S., Chatterjee, S., Das, K., & Chattopadhyay, J. (2008). Role of competition in phytoplankton population for the occurrence and control of plankton bloom in the presence of environmental fluctuation. *Ecological Model*. 220(2):96-110.
- Liu, X., and Lou, Y. (2010). Global dynamics of a predator prey model. *Journal of Mathematical Analysis and Application*. 371:323-340.
- Duggins, D.O. (1981). Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia*. 48(2):157-163.
- Rehim, M., & Mudassar, I. (2010). Dynamical analysis of a delay model of phytoplankton-zooplankton interaction. *Elsevier*. 36:638-647.
- Rice E. (1984). *Allelopathy*, Academic Press, New York.
- Rice, T.R. (1987). In: Biotic influences affecting population growth of plankton Algae. *Fishery Bulletin*. 54:288-245.
- Sarkar, R.R., & Chattopadhyay, J. (2003). The role of environmental stochasticity in a toxic phytoplankton-non-toxic phytoplankton-zooplankton system, *Environmetrics*. 14: 775–792.
- Sinha, S., Misra, O.P., & Dhar, J. (2009). Modelling a predator-prey system with infected prey in polluted environment. *Elsevier. Applied Mathematical Model*. 34:1861-1872.
- Solé, J., García-Ladona, E., Ruardij, P., & Estrada, M. (2005). Modelling allelopathy among marine algae, *Ecological Model*. 183:373–384.
- Tapaswi, P.K., & Mukhopadhyay, A. (1999). Effects of environmental fluctuation on plankton allelopathy, *Journal of Mathematical Biology*. 39: 39–58.
- Tilman, D. (1996). Biodiversity: Population versus ecosystem stability. *Ecology*; 77(2): 350-363.
- Townsend, C.R., Harper, J.D., & Begon, M. (2009). *Essentials of Ecology*. 3rdEdn. Blackwell Sciences, London U.K.
- Wallace, K.J. (2007). Classification of ecosystem services: Problems and solutions. *Elsevier*. 139(3–4):235-246.
- Wokoma, O.A.F & Friday, U. (2016). Water quality disturbances on phytoplankton composition and abundance in Mini-Ndoi Creek, Niger Delta Nigeria. *Journal of Applied Life Science International*. 4(2): 1-9.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K, ...& Watson, R. (2006). Impacts of Biodiversity loss on ocean Ecosystem services. *Science*. 314(5800): 787-790.
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci. USA*. 96: 14463-1468.