

Jensen's inequality predicts effects of environmental variation

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Many biologists now recognize that environmental variance can exert important effects on patterns and processes in nature that are independent of average conditions. Jensen's inequality is a mathematical proof that is seldom mentioned in the ecological literature but which provides a powerful tool for predicting some direct effects of environmental variance in biological systems.

Qualitative predictions can be derived from the form of the relevant response functions (accelerating versus decelerating). Knowledge of the frequency distribution (especially the variance) of the driving variables allows quantitative estimates of the effects. Jensen's inequality has relevance in every field of biology that includes nonlinear processes.

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Historically, ecologists have emphasized the importance of average environmental conditions. The concept of environmental variance is almost completely absent from the 40 foundation papers (published from 1887–1971) identified by Real and Brown¹. Through the 1960s, the word 'variance' appeared in the abstract of only about ten papers per thousand published by the Ecological Society of America (Fig. 1). However, the number of such papers has increased since then to about 50 per thousand during the 1990s. This suggests a growing recognition among ecologists that an explicit consideration of variance is essential to explain many of the important patterns and processes in nature. Jensen's inequality provides a fundamental tool for understanding and predicting consequences of variance, but it is only just beginning to be explicitly acknowledged in the primary literature²⁻⁵, and we can find no mention of Jensen's inequality in any biology or biometry textbook.

Jensen's inequality is a mathematical property of nonlinear functions. Credited to the mathematician J.L. Jensen (1859–1925), it was first described at the end of the 19th century^{6,7}. The inequality states that: for a nonlinear function, $f(x)$, and a set of x values with a mean of \bar{x} (and a variance greater than zero), the average result of $f(x)$, $\bar{f}(x)$, does not equal the result of the average, $f(\bar{x})$. When $f(x)$ is accelerating (2^{nd} derivative is positive), $\bar{f}(x)$ is greater than $f(\bar{x})$. When $f(x)$ is decelerating (2^{nd} derivative is negative), $\bar{f}(x)$ is less than $f(\bar{x})$. The sign of the difference between $\bar{f}(x)$ and $f(\bar{x})$

depends only on the form of the function (accelerating versus decelerating).

Jensen's inequality has relevance to any area of biology that includes nonlinear functions (Box 1). Here, we develop examples from physiological ecology (photosynthesis as a function of irradiance and metabolic rate as a function of temperature) and plant-herbivore interactions, but it seems that examples could be drawn just as easily from biochemistry,

ecosystem science or any biological discipline in between. At any scale, Jensen's inequality implies that environmental variance can have important and predictable biological consequences that cannot be inferred from average environmental conditions. For any nonlinear response function, environmental variance will consistently elevate or depress the response depending on the form of the function. Therefore, whenever biological systems involve nonlinear responses, the description and interpretation of environmental data should include an explicit consideration of the variance.

Variance in light regimes depresses primary production

Although photosynthetic organisms are taxonomically diverse, the biochemistry of photosynthesis is relatively highly conserved. Carbon assimilation as a function of irradiance is almost always a decelerating saturation function (e.g. Fig. 2a, 3.5, Canny *et al.*, unpublished). Furthermore, the light regime of every habitat is inherently variable because of seasonal cycles, diurnal cycles and shading from clouds and other organisms. Jensen's inequality predicts that, because the assimilation function is decelerating, this variance at temporal and spatial scales should depress net primary production compared with the expectation based upon average irradiance.

The understory light environment of closed canopy forests is particularly variable with long periods of low-level diffuse light punctuated by short periods

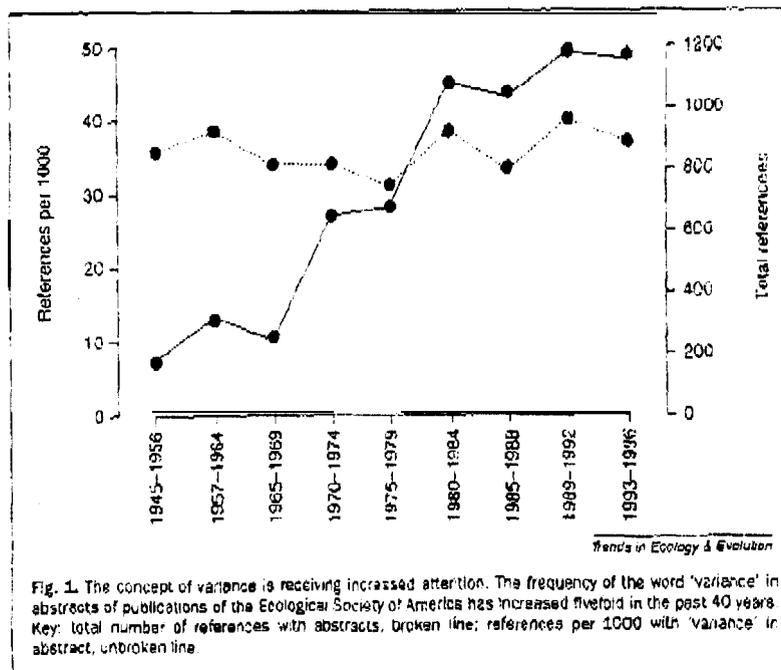
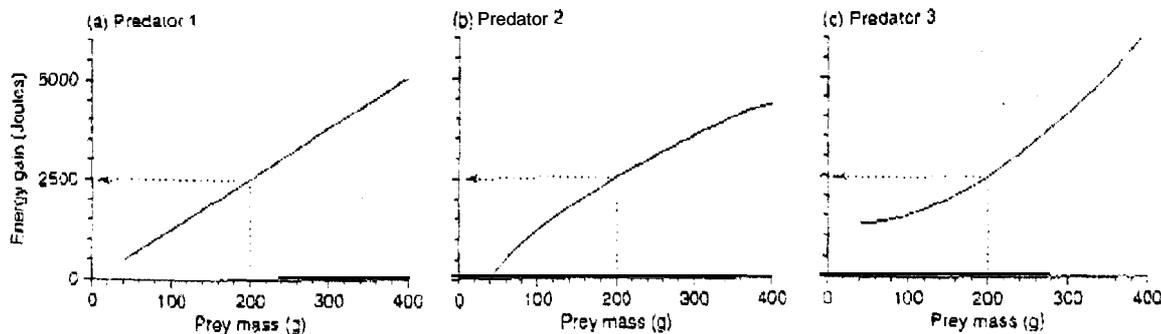


Fig. 1. The concept of variance is receiving increased attention. The frequency of the word 'variance' in abstracts of publications of the Ecological Society of America has increased fivefold in the past 40 years. Key: total number of references with abstracts, broken line; references per 1000 with 'variance' in abstract, unbroken line.

PERSPECTIVES.

Box 1. Jensen's inequality

Jensen's inequality describes how variance depresses the response variable in decelerating functions and elevates the response variable in accelerating functions. For three hypothetical predators, Figs (a)-(c), energy gained from a prey item is a function of prey mass; bigger prey yields more assimilable energy and a 200 g prey item yields 2500 J of energy. However, the functions differ in shape with the first (a) being linear, the second (b) being decelerating (concave down, 2nd derivative is negative) and the third (c) being accelerating (concave up, 2nd derivative is positive).



(Online: Fig. 1)

Trends in Ecology & Evolution

Now consider three groups of prey that each average 200 g per prey item, but differ in variance with group A being uniform, group B somewhat variable and group C highly variable (Table I). Because each group averages 200 g per prey item, does this mean that each predator would gain an average of 2500 J per prey item from consuming each prey group? No. Because the shapes of their assimilation functions differ, variable groups have different consequences for each predator (Table II).

Table I. Mass (g) of prey items in three groups (A-C)

A	B	C
200	160	80
200	180	88
200	180	120
200	220	240
200		
200	220	312
200	240	320

Table II. Average energy gain (J) per prey

	Prey group A	Prey group B	Prey group C
Predator 1	2500	2500	2500
Predator 2	2500	2490	2357
Predator 3	2500	2521	2783

Predator 1 averages 2500 J per prey item for each group because the assimilation function is linear. For any linear function, a unit increase or decrease in X results in the same magnitude change in Y. On average, predator 2 gains less energy per prey item from feeding on the variable groups because, for decelerating functions, a unit decrease in X decreases Y more than a unit increase in X increases Y. Predator 3 gains more energy per prey item from feeding on variable groups because, for accelerating functions, a unit decrease in X decreases Y less than a unit increase in X increases Y. The same phenomenon can apply to populations as well as individuals. If seven predators all had the same assimilation functions as predator 2, and each consumed one prey item from a variable group, the average energy gained per predator would be < 2500 J even though the mean prey mass is 200 g. Although the three example response curves are all increasing functions, Jensen's inequality also applies to decreasing functions. For example, a negative exponential function is a form of an accelerating function (2nd derivative is positive), so increasing variance in the X variable tends to increase the average result of the function (as in predator 3). The direction of the effect of variance on a response variable depends entirely on the form (accelerating versus decelerating) of the response function.

of high irradiance as the sun passes over gap in the canopy (sun flecks). Consider hobblebush (*Viburnum alnifolium*), a dominant understory shrub of boreal forests in northeastern North America. If the average light level for the day is used to estimate net daily assimilation, then assimilation is overestimated by >100% (Fig. 2, P.S. Canny *et al.*, unpublished). We refer to this consequence of Jensen's inequality as aggregation bias: systematic errors in the estimate of a biological response [difference between $f(x)$ and $f(\bar{x})$] that arise from averaging values of the independent variable over a scale that is coarser than that experienced by the biological system (in this case, a leaf). Plant leaves respond rapidly to changes in irradiance, so the daily carbon budgets

are estimated most accurately if irradiance is measured and recorded at time intervals of seconds to minutes. In the light environment described in Fig. 2 (D.S. Canny *et al.*, unpublished), there was enough temporal autocorrelation of irradiance such that aggregating measurements for up to 10-15 minutes produced less than a 10% error in estimated daily carbon budgets, but aggregating across 60 minutes or more produced >20% error. Aggregation bias can also be introduced by averaging across space.

For *V. alnifolium*, averaging the measurements of three light sensors spaced ten meters apart resulted in overestimation of daily carbon budgets by 14%. This illustrates the need for careful decisions about how to measure. Interpret

and report environmental variables such as irradiance. Solar input is frequently reported as a daily or monthly average. However, it is impossible to develop unbiased estimates of daily photosynthesis from average daily or monthly irradiance without making assumptions about the frequency distribution of short-term irradiance. The scale at which aggregation bias becomes severe will be a function of the spatial and temporal autocorrelation of the environmental variable, as well as the strength of nonlinearities in the response functions.

In addition to these practical considerations, Jensen's inequality has some interesting theoretical consequences for the physiological ecology of photosynthesis. For example, two environments with

the same average daily irradiance but different frequency distributions of short-term irradiance, could yield markedly different carbon budgets for physiologically identical plants. Similarly, the optimization of carbon acquisition strategies (e.g. by adjustment of the light response functions and changes in induction state) could be as strongly influenced by the variability in irradiance as by the average irradiance. Evaluating carbon acquisition strategies and the ecological consequences of changes in light regime requires a careful separation of effects caused by leaf physiology versus the mathematical effects of Jensen's inequality.

Variance in temperature affects animal metabolism

The metabolic rates of poikilotherms tend to increase exponentially as a function of temperature. The accelerating form of these functions implies that variance in temperature will elevate poikilotherm metabolic rates. Temperature regimes, like irradiance regimes, are inherently variable but differ in that temperatures tend to approximate a normal distribution⁹ in an environment where the standard deviation in operative temperatures (i.e. body temperature,) is 3–8°C, metabolic rates would be 3–50% greater than in a constant thermal regime with the same average temperature (Fig. 3). The combination of a high Q_{10} (i.e. the factor by which metabolic rate increases over 10°C) and high thermal variation might be selected against because of these rather dramatic increases in maintenance energy requirements. There are predictable patterns in the variability of environmental temperatures. Arid environments and high-altitude environments tend to have very high diurnal variance in air temperatures. Arboreal habitats are more variable than soil habitats, and terrestrial habitats are more variable than aquatic habitats. We predict that poikilotherms adapted to more variable environments will be more likely to employ behavioral thermoregulation (such as microhabitat choice) to minimize variance in their operative body temperatures and will tend to have a lower Q_{10} than related species from low-variance environments. Seasonal changes in behavior and temperature physiology may represent adaptations to minimize the increases in maintenance metabolism that are introduced by seasonal variability in environmental temperature.

The metabolic rate of homeotherms as a function of environmental temperature has a fundamentally different form from that of poikilotherms. Metabolic rates of homeotherms tend to increase both above and below a thermoneutral zone. The slope increases with increasing

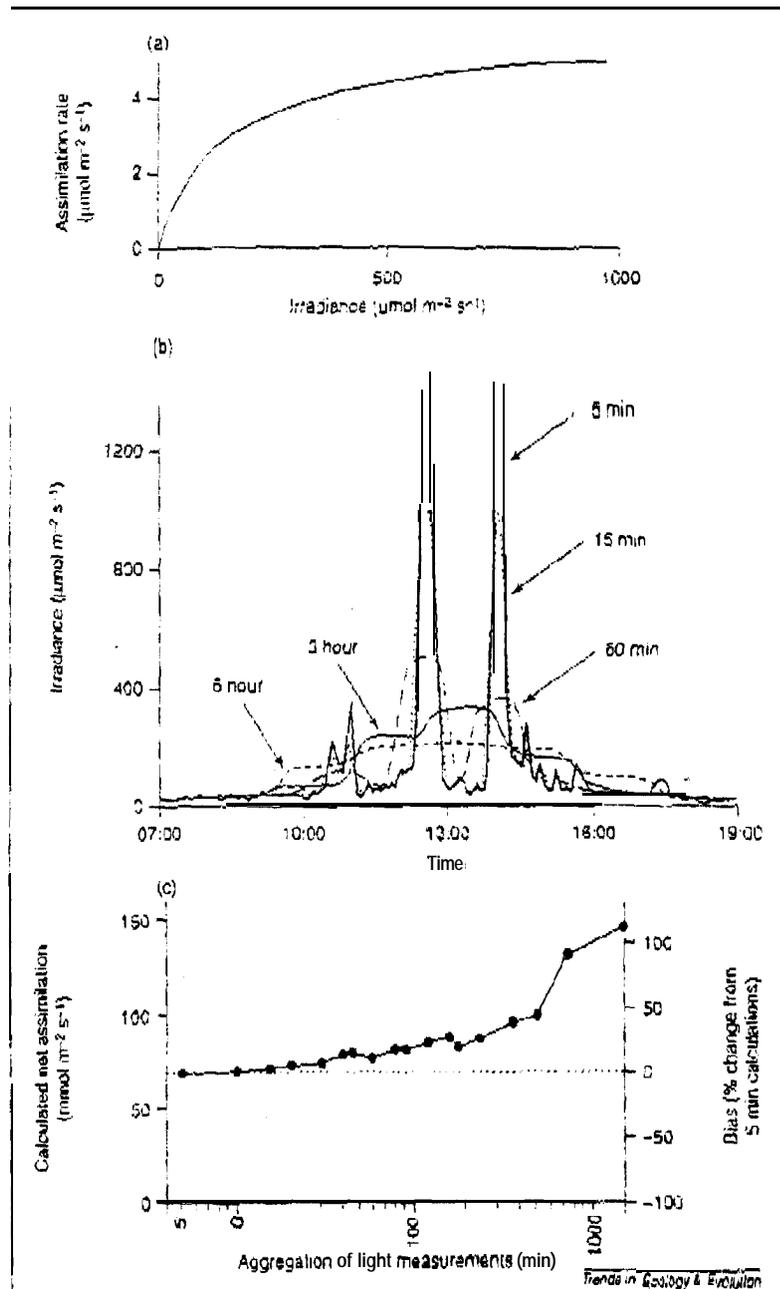


Fig. 2. As with most photosynthetic organisms, carbon assimilation (A) by hollyhock, *Viburnum alnifolium*, increases with irradiance as a decelerating function (a). In this case, $A = b \cdot I^a / (1 + a \cdot I)$, where $a = 0.0074$, $b = 0.044$, and $Resp = 0.22$. (b) The light regime of *V. alnifolium*'s understory habitat is variable on a timescale of minutes. The irradiance measurements for one day averaged across intervals of 5 min, 15 min, 30 min, and 60 min show how aggregation of measurements dampens the temporal variation in irradiance. (c) Net carbon assimilation for the day can be calculated based on any temporal aggregation of light measurements from 5 min to 1 day. Because of Jensen's inequality, aggregating light measurements produced a systematic bias in calculated net assimilation. Daily carbon assimilation was overestimated by >twofold using the 24-h average instead of the 5 min measurements. Light response and irradiance data from Canny et al., unpublished.

temperature around both ends of the thermoneutral zone (slope goes from negative to zero at the lower critical temperature and from zero to positive at the upper critical temperature), so why temperature variation spans either the

upper or lower critical temperature average metabolic rate will be greater than in a constant thermal regime with the same average temperature. Therefore, temperature variability tends to have the same qualitative effect on

PERSPECTIVES

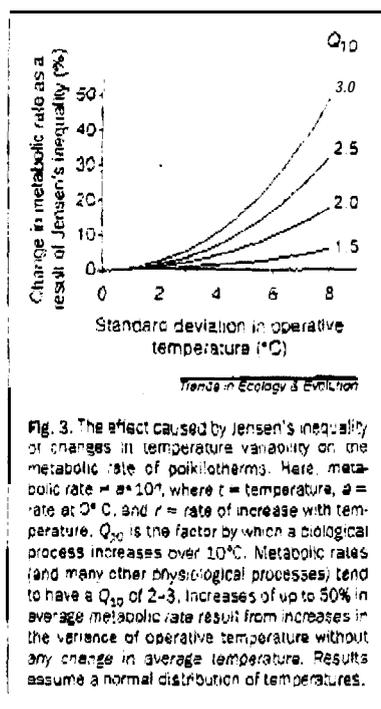


Fig. 3. The effect caused by Jensen's inequality of changes in temperature variability on the metabolic rate of poikilotherms. Here, metabolic rate = $a \cdot 10^{bt}$, where t = temperature, a = rate at 0°C, and b = rate of increase with temperature. Q_{10} is the factor by which a biological process increases over 10°C. Metabolic rates (and many other physiological processes) tend to have a Q_{10} of 2–3. Increases of up to 50% in average metabolic rate result from increases in the variance of operative temperature without any change in average temperature. Results assume a normal distribution of temperatures.

metabolism maintenance in homeotherms as in poikilotherms.

Poikilotherm development rate is also a nonlinear function of temperature. The generalized temperature response function is "accelerating at low temperatures, approximately linear at intermediate temperatures and decelerating at high temperatures". Consequently, the effects of temperature variation as a result of Jensen's inequality will tend to be positive at low temperatures, minimal at intermediate temperatures and negative at high temperatures. These effects are a recognized source of error in degree-day models of insect development and plant phenology, and have been referred to as the Kaufmann effect¹¹. We hypothesize that differences among environments in temperature variability will select for changes in the acceleration rate, inflection point and deceleration rate of poikilotherm developmental responses to temperature. These evolutionary responses would have the effect of altering subsequent phenotypic responses to changes in temperature variability. If so, the same change in temperature variance could have different ecological effects on, for example, aquatic insects versus terrestrial insects.

Herbivores encounter variable hosts

Intraspecific variance in host tissue quality is common^{12–16}. The causes of variance in foliage quality include microsite and genetic differences between plants, plant ontogeny, leaf ontogeny, inducible responses and somatic mutation^{13,14,17–19}.

Insect responses to this variance include selective feeding, modified consumption rates and the evolution of locally adapted demes^{20–22}.

Although variance in host quality can affect herbivores in many ways, we will discuss only how variance in the ingested tissue affects herbivore performance via Jensen's inequality. The variance actually experienced by a herbivore is a function of the scale at which variability occurs, the mobility of the herbivore and the discrimination capacity of the herbivore. Host tissue quality can vary among plant populations, plants within a population, leaves within a plant and even areas within a single leaf^{20,23,24}. Variability beyond the scale of foraging by an individual will tend to exert its effects at the population level (e.g. if fecundity as a function of leaf chemistry is nonlinear, then mean population fecundity will differ from that predicted from the mean leaf chemistry). Variability at a finer scale can exert effects at the level of the individual (e.g. if development time as a function of leaf chemistry is nonlinear, then development time for an individual can differ from that predicted by the average chemistry of ingested leaves). Behavioral responses that allow herbivores to exploit resources with higher average tissue quality^{16,20,25} will tend to reduce the variance experienced by the herbivores. Such behaviors reduce the impact of Jensen's inequality, but do not eliminate it unless the realized variability is reduced to zero. It is also possible that other behaviors actually increase the variance experienced by the herbivore and hence increase the importance of Jensen's inequality.

Insect herbivores are affected by host variance in nitrogen

Insect growth performance as a function of dietary nitrogen concentration, [N], is often nonlinear^{21,26}. This implies that variance in host [N] has direct consequences for insect herbivores. The responses are decelerating saturation functions for the southern armyworm (*Spodoptera eridania*) and gypsy moth (*Lymantria dispar*)^{21,27}. In these cases, variance in [N] should depress performance and this has been experimentally demonstrated for gypsy moths². In the western spruce budworm (*Choristoneura occidentalis*), the response functions for survival and female pupal mass are complex, accelerating at low [N] and decelerating at high [N]²⁶. Therefore, the effect of host variance on budworm performance would tend to be positive at low average [N] and negative at high average [N]. Insect growth performance can also be linear²⁷, in which case there are no direct effects of variance in dietary nitrogen. Variance in [N] can exert direct effects on herbivores,

but the magnitude and direction of the effects will differ among taxa because taxa differ in the shape of their response functions.

Insect herbivores are affected by host variance in secondary metabolites

Herbivore performance as a function of secondary metabolite concentrations also includes a range of functions from linear to complex (having both accelerating and decelerating regions)^{28–33}. For example, growth rate and survival of the leaf beetle (*Chrysomela falsa*) decreased linearly with condensed tannins from birch (*Betula resinifera*)²⁹. Oviposition success of the southern pine beetle (*Dendroctonus frontalis*) was a negative exponential (accelerating) function of tree resin flow³³. Survival of the cabbage looper (*Trichoplusia ni*) was a decreasing decelerating function of diester concentration²⁸. Larval mass of the tobacco budworm (*Heliothis virescens*) declined with increasing concentrations of two different diterpene acids but the functions were decelerating at low levels and accelerating at higher levels³².

The fact that many of these response functions are nonlinear suggests that variance in host secondary metabolite concentrations has direct consequences for herbivores. In the studies we examined, the performance response of herbivores to secondary metabolite concentrations tended to be accelerating functions rather than decelerating functions (ten cases of accelerating functions versus three decelerating functions, two complex functions and eight linear functions). This suggests that many herbivores will benefit from variance in secondary metabolite concentrations because of Jensen's inequality. In some systems, Jensen's inequality could result in selection for plants to decrease variance (perhaps by distributing resources evenly). Karban *et al.*³ suggested that induced defenses in plants are a means of elevating variance in host tissue that are selectively favored because of Jensen's inequality. If so, induced defenses should be most common in systems where herbivore performance is a decelerating function of metabolite concentration.

The form of insect response functions is relevant to plant breeding and pest management. In the case of cotton (*Gossypium hirsutum*), herbivore performance tends to decline with allelochemical concentrations³⁰, so deploying strains of cotton with a high average concentration of allelochemicals could reduce damage by insects. However, because herbivore performance tends to decline as a negative exponential function (an accelerating function) and plant tissue concentrations tend to be variable, the reduction in

herbivory would be less than expected based on mean concentrations of allelochemicals.

The shape of herbivore performance functions could change with evolutionary time. Because of physiological and biochemical constraints, we expect that changes in the slope of performance functions and shifts in the function peaks will be more common than changes from decelerating to accelerating or vice versa. If evolutionary and behavioral responses to host variance do not commonly change the sign of the 2nd derivative of a performance function (i.e. accelerating versus decelerating), they cannot influence the direction of the effect of host variance on a herbivore.

Variable phytochemistry and the frequency of nonlinear responses by herbivores to phytochemistry suggest a strong role for Jensen's inequality in plant-herbivore interactions. Simple simulations can calculate the effects of Jensen's inequality: these only require estimates of the response function and of the frequency distribution of the driving variable. In general, the magnitude of Jensen's inequality will increase with increasing nonlinearity (absolute value of the 2nd derivative) and increasing variance in the driving variable, but many response functions will be more complex than a simple exponential model and many environmental variables have non-normal distributions. In these cases, there is probably no substitute for simulations developed around empirical frequency distributions. The net effect of host variance depends on the combination of the response functions for all relevant compounds and, for a given herbivore, the shapes of these functions might differ for different host compounds. Simulations can be developed around response surface models¹⁴ whenever herbivore performance is influenced by interactions among host traits (e.g. when there are interacting effects of dietary nitrogen and secondary metabolites²⁵).

Conclusions and prospects

Jensen's inequality deserves consideration in many more areas of ecological research than we have discussed here. For example, photosynthesis is a decelerating function of temperature and many plants respond to increased atmospheric carbon dioxide concentration (CO₂) with increased maximum assimilation, a shift in the optimal temperature and a narrowing of the peak in the temperature response²⁶. One consequence suggested by Jensen's inequality is that natural variance in temperature will cause a greater depression in assimilation under increased [CO₂] than at ambient [CO₂] because of

the narrowing of the peak. Estimated effects based solely on maximum assimilation or assimilation at a given temperature will overestimate the effect of increased [CO₂].

In any system in which nonlinear processes are common, Jensen's inequality describes and predicts direct implications of environmental variance. A dominant theme in ecosystem science is the development of models that can be driven by readily obtained data, such as monthly average temperatures, but can still capture the behavior of dynamic biological systems that are sometimes intrinsically nonlinear¹⁷. With estimates of the response functions and the variance experienced, Jensen's inequality can be used to estimate the error involved in averaging at different scales and aid in choosing the appropriate scale for calculation steps in the model.

Because resources are often distributed unevenly (spatial variance), Jensen's inequality has been implicated in explanations of saltatory search and risk-sensitive foraging²⁴ in population ecology, functional responses, numerical responses and intraspecific interference tend to be nonlinear and population densities are often aggregated and highly variable²⁸. Results of stochastic population models will systematically differ from results of equivalent deterministic models whenever the models include nonlinearities²⁹. Community ecology includes extensive consideration of nonlinearities in species interactions and evolutionary ecology involves the study of nonlinear fitness surfaces.

In conclusion, Jensen's inequality has broad relevance for understanding the effects of environmental variance on ecological and evolutionary processes. It deserves consideration whenever a study system includes nonlinear processes. The inequality is not a biological phenomenon *per se* but instead a mathematical consequence of the nonlinear form of many biological functions and the variance inherent in many environmental factors. Progress in our understanding of the role of environmental variance in ecology and evolution will be accelerated if Jensen's inequality becomes as familiar to ecologists as the central limit theorem.

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References

- 1 Real, L.A. and Brown, J.H. (1991) *Foundations of Ecology*. University of Chicago Press
- 2 Stockhoff, B.A. (1993) Diet heterogeneity: implications for growth of a generalist herbivore, the gypsy moth, *Ecology* 74, 1939-1949
- 3 Smallwood, P.D. (1996) An introduction to risk sensitivity: the use of Jensen's inequality to clarify evolutionary arguments of adaptation and constraint, *Am. Zool.* 36, 352-401
- 4 Anderson, J.P., Stephens, D.W. and Dunbar, S.R. (1997) Saltatory search: a theoretical analysis, *Behav. Ecol.* 8, 307-317
- 5 Karban, R., Agrawal, A.A. and Mani, M. (1997) The benefits of induced defenses against herbivores, *Ecology* 78, 1351-1355
- 6 Hölder, O. (1889) Ueber einen Mittelwertsatz, *Göttinger Nachr.* 38-47
- 7 Jensen, J.L. (1906) Sur les fonctions convexes et les inégalités entre les valeurs moyennes, *Acta Math.* 30, 175-193
- 8 Chazdon, R.L. and Pearcy, R.W. (1986) Photosynthetic responses to light variation in rainforest species II. Carbon gain and photosynthetic efficiency during lightflecks, *Oecologia* 69, 524-531
- 9 Ayres, M.P. and Scriber, J.M. (1994) Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae), *Ecol. Monogr.* 64, 465-482
- 10 Sparpe, P.J.H. and DeMichele, D.W. (1977) Reaction kinetics of polyklotherm development, *J. Theor. Biol.* 64, 849-870
- 11 Worner, S.P. (1992) Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect, *Environ. Entomol.* 21, 689-699
- 12 Dirzo, R. and Harper, J.L. (1982) Experimental studies on slug-plant interactions. III. Differences in the acceptability of individual plants of *Trifolium repens* to slugs and snails, *J. Ecol.* 70, 101-117
- 13 Whitham, T.G. and Slobodkinoff, C.N. (1981) Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants, *Oecologia* 49, 287-292
- 14 Schultz, J.C., Nothnagel, P.J. and Baldwin, I.T. (1982) Seasonal and individual variation in leaf quality of two northern hardwood species, *Am. J. Bot.* 69(5), 753-759
- 15 Denno, R.F. and McClure, M.S. (1983) *Variable Plants and Herbivores in Natural and Managed Systems*, Academic Press
- 16 Edwards, P.B. et al. (1990) Mosaic resistance in plants, *Nature* 347, 434
- 17 Lightfoot, D.C. and Whitford, W.G. (1989) Interplant variation in creosote bush foliage characteristics and canopy arthropods, *Oecologia* 81, 166-175
- 18 Karban, R. and Baldwin, I.T. (1997) *Induced Responses to Herbivory*, University of Chicago Press
- 19 Kearsley, M.J.C. and Whitham, T.G. (1997) The developmental stream of cottonwoods affects ramet growth and resistance to galling aphids, *Ecology* 79, 178-191
- 20 Niemelä, P., Tuomi, J. and Siren, S. (1984) Selective herbivory on mosaic leaves of variegated *Acer pseudoplatanus*, *Experientia* 40, 1433-1434

PERSPECTIVES

- 21 Korowe, D.N. and Martin, M.M. (1989) The effects of quantity and quality of diet nitrogen on the growth efficiency of food utilization nitrogen budget and metabolic rate of fifth-instar *Spodoptera eridania* larvae (Lepidoptera: Noctuidae). *J. Insect Physiol.* 35, 699-708
- 22 Mopper, S. (1996) Adaptive genetic structure in phytophagous insect populations. *Trends Ecol. Evol.* 11, 235-238
- 23 Suomela, J. and Ayres, M.P. (1994) Within-tree and among-tree variation in leaf characteristics of mountain birch and its implications for herbivory. *Oikos* 70, 212-222
- 24 Suomela, J., Ossipov, V. and Haukioja, E. (1995) Variation among and within mountain birch trees in foliage phenols, carbohydrates, and amino acids, and in growth of *Epirrita autumnata* larvae. *J. Chem. Ecol.* 21, 1421-1446
- 25 Price, P.W. (1994) Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. *Res. Popul. Ecol.* 36, 3-14
- 26 Clancy, K.M. (1992) Response of western spruce budworm (Lepidoptera: Tortricidae) to increased nitrogen in artificial diets. *Environ. Entomol.* 21, 331-344
- 27 Ayres, M.P., Suomela, J. and Maclean, S.F., Jr (1987) Growth performance of *Epirrita autumnata* (Lepidoptera: Geometridae) on mountain birch trees, broods, and tree x brood interactions. *Oecologia* 74, 450-457
- 28 Byers, R.A., Gustine, D.L. and Mayer, B.C. (1977) Toxicity of β -nitropropionic acid to *Trichoplusia ni*. *Environ. Entomol.* 6, 229-232
- 29 Ayres, M.P. et al. (1997) Diversity of structure and anti-herbivore activity in condensed tannins. *Ecology* 78, 1696-1711
- 30 Jenkins, J.N. et al. (1983) Cotton allelochemicals and growth of tobacco budworm larvae. *Crop Sci.* 23, 1195-1198
- 31 Parr, J.C. and Thurston, R. (1972) Toxicity of nicotine in synthetic diets to larvae of the tobacco hornworm. *Ann. Entomol. Soc. Am.* 65, 1185-1188
- 32 Elliger, C.A. et al. (1976) Diterpene acids as larval growth inhibitors. *Experientia* 32, 1364-1366
- 33 Reeve, J.D., Ayres, M.P. and Lorio, P.L., Jr (1995) Host suitability, predation, and bark beetle population dynamics. In *Population Dynamics: New Approaches and Synthesis* (Cappuccino, N. and Price, P.W., eds), pp. 339-357. Academic Press
- 34 Clancy, K.M. and King, R.M. (1992) Defining the western spruce budworm's nutritional niche with response surface methodology. *Ecology* 74, 442-454
- 35 Siansky, F. and Wheeler, G.S. (1992) Caterpillars compensatory feeding response to diluted nutrients leads to toxic allelochemical dose. *Entomol. Exp. Appl.* 65, 171-186
- 36 Berry, J. and Bjorkman, O. (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.* 31, 491-543
- 37 Aber, J.D. and Federer, C.A. (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92, 463-474
- 38 Folt, C.L. and Schulze, P.C. (1993) Spatial patchiness, individual performance and predator impacts. *Oikos* 69, 560-566
- 39 Chesson, P.L. (1981) Models of spatially distributed populations: the effect of within-patch variability. *Theor. Popul. Biol.* 19, 288-325