



Common Dynamic Structure of Canada Lynx Populations Within Three Climatic Regions

Nils Chr. Stenseth, *et al.*

Science **285**, 1071 (1999);

DOI: 10.1126/science.285.5430.1071

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of September 12, 2011):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/285/5430/1071.full.html>

This article **cites 11 articles**, 2 of which can be accessed free:

<http://www.sciencemag.org/content/285/5430/1071.full.html#ref-list-1>

This article has been **cited by** 104 article(s) on the ISI Web of Science

This article has been **cited by** 8 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/285/5430/1071.full.html#related-urls>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

exclusion was assessed by *t* tests, treating each year as a separate comparison. The survival on control trees versus outside cages on experimental trees was not significantly different (apart from fall of 1992), so we treated these replicates as a single category, "exposed." Our main result was not affected by this data pooling, because in 1993, the first year after the peak, survival inside cages was significantly higher than survival both outside cages on experimental trees and on control trees ($P < 0.001$ for both comparisons). The comparisons in the ratio of increase were performed in the same manner, except the data were first log-transformed to stabilize the variance.

19. The difference in survival inside and outside of the cages was not statistically significant in 1994, the second decline year. This was probably because of lower intraspecific competition outside of the cages due to lower egg density there (17). There was a significant negative effect of egg density on

survival inside exclusion cages (linear regression: $F_{1,51} = 9.38, P < 0.0035$). When we corrected survival rates by taking intraspecific effects into account using this relation, we found a significant difference in survival, suggesting that the predation impact on survival was still detectable 2 years after the peak.

20. C. W. Berisford, in *The Southern Pine Beetle. USDA-Forest Service Technical Bulletin 1631*, R. C. Thatcher, J. L. Searcy, J. E. Coster, G. D. Hertel, Eds. (U.S. Department of Agriculture, Washington, DC, 1980), pp. 31–54.
21. J. D. Reeve, *Oecologia* **112**, 48 (1997).
22. J. D. Reeve, J. A. Simpson, J. S. Fryar, *J. Entomol. Sci.* **31**, 123 (1996).
23. W. W. Murdoch, R. N. Nisbet, S. P. Blythe, W. S. C. Gurney, J. D. Reeve, *Am. Nat.* **129**, 263 (1987).
24. H. C. J. Godfray and M. P. Hassell, *J. Anim. Ecol.* **58**, 153 (1989).

25. S. L. Pimm, *The Balance of Nature?* (Univ. of Chicago Press, Chicago, IL, 1991).
26. W. S. C. Gurney and R. M. Nisbet, *Ecological Dynamics* (Oxford Univ. Press, New York, 1998).
27. C. J. Krebs *et al.*, *Science* **269**, 1112 (1995).
28. P. J. Hudson, A. P. Dobson, D. Newborn, *ibid.* **282**, 2256 (1998).
29. T. L. Payne, in (20), pp. 7–30.
30. J. D. Reeve, D. J. Rhodes, P. Turchin, *Ecol. Entomol.* **23**, 433 (1998).
31. This research was supported by USDA-Forest Service RWU-4501 and by NSF grant DEB 9509237. We thank D. Rhodes and the staff of Kisatchie National Forest for assistance in the field. J. Elkinton, J. Hayes, J. Cronin, A. Berryman, and C. Godfray provided helpful comments and suggestions on an early version of the manuscript.

15 April 1999; accepted 21 June 1999

Common Dynamic Structure of Canada Lynx Populations Within Three Climatic Regions

Nils Chr. Stenseth,^{1,2*} Kung-Sik Chan,³ Howell Tong,^{4,5}
 Rudy Boonstra,^{1,6} Stan Boutin,⁷ Charles J. Krebs,^{1,8} Eric Post,²
 Mark O'Donoghue,^{8,9} Nigel G. Yoccoz,^{1,10}
 Mads C. Forchhammer,^{11,12} James W. Hurrell¹³

Across the boreal forest of Canada, lynx populations undergo regular density cycles. Analysis of 21 time series from 1821 onward demonstrated structural similarity in these cycles within large regions of Canada. The observed population dynamics are consistent with a regional structure caused by climatic features, resulting in a grouping of lynx population dynamics into three types (corresponding to three climatic-based geographic regions): Pacific-maritime, Continental, and Atlantic-maritime. A possible link with the North Atlantic Oscillation is suggested.

Periodic population fluctuations of the Canada lynx (*Lynx canadensis*) have greatly influenced both ecological theory and statistical time series modeling [(1, 2); see (3) for a summary]. Recent analyses have focused on the extent of synchrony in population fluctuations, assessing the importance of external abiotic factors (such as weather) and internal biotic factors (such as dispersal among populations) in causing spatial patterns (4). Such empirical and theoretical approaches have, however, assumed that the populations were structurally similar [that is, the density-dependent relationships are identical among populations (5)]. This assumption has never been thoroughly evaluated. To do so requires determining whether the lynx populations display the same phase- and density-dependent structure (3) and then searching for similar underlying causes of the observed dynamics. Using new statistical methods developed for this purpose (6), we ask to what extent the time series on the Canada lynx (Fig. 1) compiled by the Hudson Bay Company for the period 1821 to 1939 (7) and the corresponding more modern time series com-

pared by Statistics Canada for the period 1921 to present (8), taken together, are structurally similar. Specifically, we ask whether the phase- and density-dependent structure of changes in lynx abundance cluster into groups defined according to ecological-based features (9) or according to climatic-based features (10, 11).

The available time series (Fig. 1A) cover two ecosystems (referred to below as ecological regions): the northern, open boreal forest (Fig. 1B) and the southern, closed boreal forest. In western Canada, the mountainous topography adds complexity. Additionally, the series cover three climatic regions defined by the spatial influences of the North Atlantic Oscillation (NAO) [Fig. 1C; see (12)], which may contribute to spatial differences in trophic interactions (13).

Previously, we fitted a piecewise linear autoregressive model (14) to each of the series (3). A general hare-lynx model (3, 15) may be expressed as an equivalent model in delay coordinates of the lynx (the species for which we have data). Here we check whether all the time series, or some subsets of these,

display the same underlying phase- and density-dependent structure. For this purpose we use a piecewise linear model (14, 15):

$$y_{s,t} = \begin{cases} \beta_{s,1,0} + \beta_{s,1,1}y_{s,t-1} + \beta_{s,1,2}y_{s,t-2} + \varepsilon_{s,1,t} & y_{s,t-d} \leq \theta_s \\ \beta_{s,2,0} + \beta_{s,2,1}y_{s,t-1} + \beta_{s,2,2}y_{s,t-2} + \varepsilon_{s,2,t} & y_{s,t-d} > \theta_s \end{cases} \quad (1)$$

where $y_{s,t}$ is the log-transformed abundance of lynx at site s and for year t [that is, $y_{s,t} = \log(Y_{s,t})$ where $Y_{s,t}$ is the abundance of lynx at site s and in year t , and where $s = 1, 2, \dots$, represent the sites corresponding to the individual time series; see Fig. 1A]; $\beta_{s,j}$ are the statistical parameters that determine the phase- and density-dependent structure of the system ($i = 1$ and 2 correspond to the lower and the upper regimes of the model; $j = 0, 1, 2$ correspond to the constant term, the first lag, and the second lag, respectively) at site s ; $\varepsilon_{s,i,t}$ is normally distributed, time-independent noise [$N(0, \sigma^2_{s,i})$]; and θ_s is the threshold applicable to the log-transformed density d years earlier.

¹Center for Advanced Study, The Norwegian Academy of Science and Letters, Drammensveien 78, N-0271 Oslo, Norway. ²Division of Zoology, Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway. ³Department of Statistics and Actuarial Science, University of Iowa, Iowa City, IA 52242, USA. ⁴Department of Statistics, London School of Economics, London WC2A 2AE, UK. ⁵Department of Statistics, University of Hong Kong, Hong Kong. ⁶Division of Life Sciences, University of Toronto at Scarborough, Scarborough, Ontario M1C 1A4, Canada. ⁷Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. ⁸Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada. ⁹Department of Renewable Resources, Fish and Wildlife Branch, P.O. Box 310, Mayo, Yukon Y0B 1M0, Canada. ¹⁰Department of Arctic Ecology, Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway. ¹¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK. ¹²Department of Landscape Ecology, National Environmental Research Institute, Kalø, Grenåvej 12, DK-8410 Rønne, Denmark. ¹³National Center for Atmospheric Research, Climate Analysis Section, P. O. Box 3000, Boulder, CO 80307–3000, USA.

*To whom correspondence should be addressed. E-mail: n.c.stenseth@bio.uio.no

Such a threshold approach has several statistical advantages (16). The upper (respective lower) regime has been found to correspond to the decrease (respective increase) phase (3).

Because of varying carrying capacities and trapping efforts across sites, we expect series to have different means and standard deviations. Therefore, Chan *et al.* (6) considered the hypothesis of common structure that all series enjoy the same dynamics up to their means and standard deviations. The hypothesis of common structure is equivalent to two hypotheses: the hypothesis of common slopes $\beta_{s,i,j} = \beta_{1,i,j}$, and the hypothesis of common ratio of intercepts [(the intercept in the upper regime)/(the intercept in the lower regime)] takes the same value at the threshold across the different sites. Chan *et al.* (6) derived some test statistics for checking these hypotheses.

We also compared model fits between various possible groupings of the time series into subgroups. The SETAR (self-exciting threshold autoregression) models (Eq. 1) may be constrained to have some coefficients identical across series within a given subgroup. Different groupings can be compared in terms of their respective AICs (Akaike information criteria) (14, 17). For groupings involving different series to be comparable, each grouping will be defined for all series. A model with minimal AIC strikes a good balance between parsimony and goodness of fit to the data.

Time series coming from the same locations exhibit the same dynamic structure, indicating a common underlying dynamic model (18). The time series come from forested biomes across Canada and thus from areas with greatly different plant species composition and habitat structure. Focusing on the vegetation, we may classify the time series into two ecological-based groups (Fig. 1B): the northern forest tundra, which consists of shrub tundra and low-density trees (19), and the true boreal forest, which is a mixture of conifer and deciduous trees (19). [A western ecological-based group with heterogeneous topography and habitat, as well as climate (20) may also be identified.] However, treating the old and modern series separately, the ecological-based grouping represents no improvement over the baseline of no grouping [Table 1; see also (21, 22)].

As an alternative to this ecological-based grouping, the Canada lynx series may be grouped according to three major climate-based features: the Pacific-maritime region, the Continental region, and the Atlantic-maritime region (Fig. 1C). This grouping clearly provides a better description of the data [Table 1; see also (22)]. The similarity is particularly strong for the decrease phase. There is evidence in support of climate-based properties contributing to the structuring of the lynx dynamics.

Over much of central and western Cana-

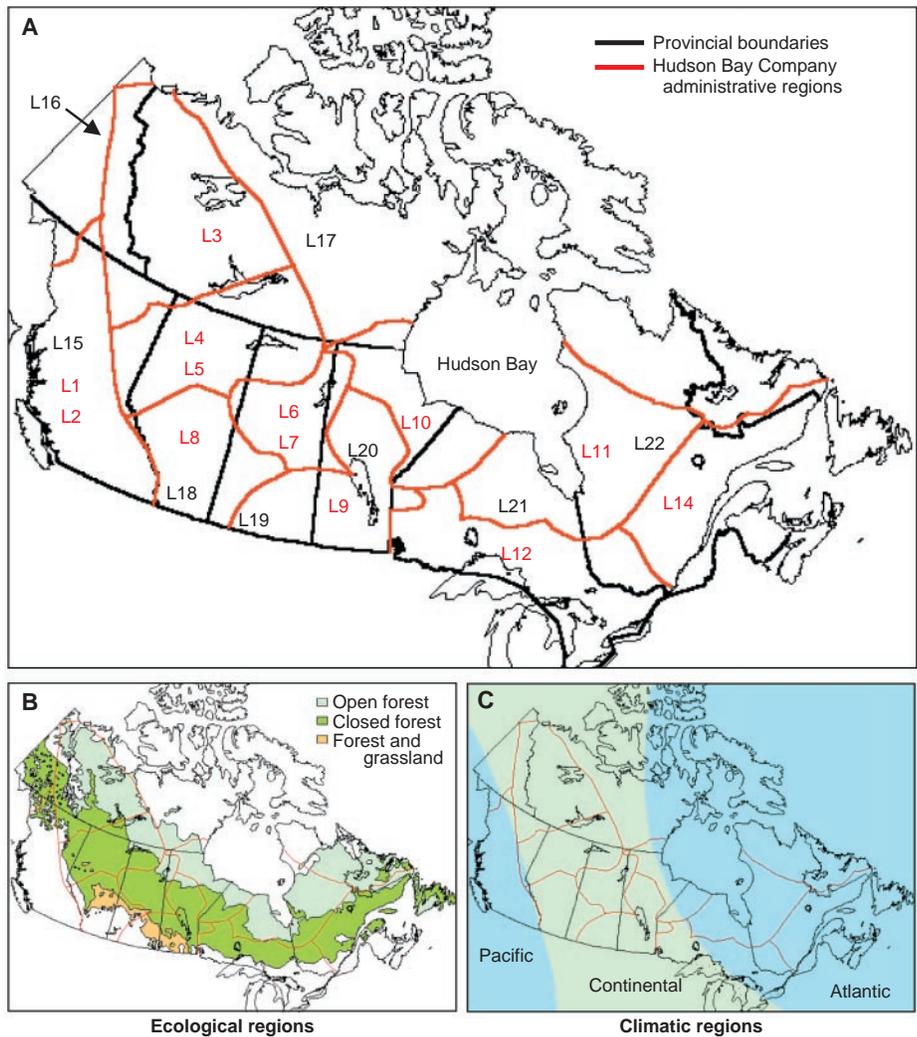


Fig. 1. Time series data studied. (A) Map of Canada with demarcations of the studied time series [red indicates the Hudson Bay Company time series (7) and black indicates the recent series (8)]. See (3) for definitions of names of the individual time series used. (B) Ecological regions of Canada (24). (C) Climatic regions of Canada (10). The NAO refers to a meridional oscillation in surface pressures with centers of action near Iceland and over the subtropical Atlantic. When surface pressures are lower than normal near Iceland and higher than normal over the subtropical Atlantic (the positive phase of the NAO), enhanced northerly flow over eastern Canada cools surface temperatures and enhanced southerly flow from the Gulf of Mexico into much of central Canada produces warm surface anomalies. Over the Pacific-maritime region, there is no significant NAO signature.

da, surface climate is most strongly influenced by the atmospheric circulation upstream over the North Pacific and in particular by a natural mode of large-scale atmospheric variability known as the Pacific–North American (PNA) teleconnection pattern (23). However, the influence of the PNA on Canadian surface temperature is spatially homogeneous. In contrast, the influence of the NAO on surface winter temperatures varies considerably from coast to coast (Fig. 1C) and shows spatial variation corresponding well to the best grouping of the lynx series (Table 1). Hence, it is the winter atmospheric circulation, for which the NAO may serve as a proxy, that probably contributes to making the nonlinear structure of the hare-lynx dynamics similar within each of the three Ca-

nadian groups. Although it is generally known that climate profoundly influences regional variation in vegetation [for example, see (9)], our results suggest that the spatio-temporal patterns of climatic variation also influence the trophic interaction between the lynx and its main prey, the snowshoe hare, differently across these regions.

Because the NAO may have a delayed effect on the lynx dynamics, we have to choose between using lag-0 or lag-1 NAO as the covariate. Several statistical techniques are available, including Cox’s test of separate families of hypotheses, AIC or its many variants, and others (17). Even though the effect of the NAO on lynx abundance is not strong, the lynx series fall along an east-west gradient progressing from negative to positive and

Table 1. Common structure in the underlying dynamics. Groupings with the smallest AIC value represent the best ones. (Only the AIC differences between the particular grouping and the baseline comparison are given [see (22), where the absolute AIC values are also given]. In some of the subgroups, the SETAR models are constrained to have some coefficients identical across series within the subgroup (see "Identical constraint structure" column). These constraints are suggested by the new statistical tests developed by Chan *et al.* (6). For different groupings involving different series to be comparable, each grouping is defined for all series in the panel; each series not in a grouping implicitly forms a singleton group. For definition of names of the series (L1, L2, ..., L22), see (3).

Groupings	Group definitions	AIC difference*	Identical constraint structure†
Baseline comparison			
No groupings	(Individual series without any constraints) (L1), (L2), ... (L14), (L15), ... (L22)	0	
Old and modern as separate groupings	All Hudson Bay Co. series (L1, L2, ..., L14) All Statistics Canada series (L15, L16, ..., L22)	-28.12	1
Old and modern grouped together	All series together (L1, L2, L3, ..., L22)	-21.36	1
Ecological-based grouping			
	Western (L1, L2) (L15)	-28.75 (-20.25)	2
	Northern (L3, L10) (L16, L17)		3 1
	Southern (L4, L5, L6, L7, L9) (L18, L19, L20)		1 3
	Eastern (L11, L12, L14) (L21, L22)		1 1
Climate-based grouping (maritime vs. continental)			
	Pacific-maritime (L1, L2) (L15)	-32.14 (-23.39)	2
	Continental (L3, L4, L5, L6, L7, L9, L10) (L16, L17, L18, L19, L20)		1 3
	Atlantic-maritime‡ (L11, L12, L14) (L21, L22)		3 3

*AIC differences given in parentheses correspond to assuming only constraints on lag-1 and lag-2 in the upper regime. †1, $\beta_{s,2,1}$ and $\beta_{s,2,2}$ each being common for different series (different s); 2, $\beta_{s,i,j}$ for each *i* and each *j* being common for different series (different s); 3, $\beta_{s,1,2}$, $\beta_{s,2,1}$, and $\beta_{s,2,2}$ each being common for different series (different s). ‡The old and modern series in the Eastern (Atlantic-maritime) seem to share the same lag-1 and lag-2 coefficients in the decrease phase, as imposing these constraints further decreases the AIC by 3.39 for both groupings.

finally to no effect of the NAO. The previously observed phase-dependent nature of the density-dependent structure (3) remains even after the NAO is included as a covariate. As a result, this study is consistent with earlier results but adds the geographic component to the structure of the lynx time series.

We can now reach a comprehensive synthesis of the time series of the Canadian lynx—namely, the lynx cycle is a direct result of trophic interactions varying structurally in three different regions of Canada, a grouping that is associated with the large-scale climatic effects known to be associated with the NAO. We argue that the extensive similarity during the decrease phase is to a large extent a result of region-specific winter conditions and suggest that these may be linked to the state of NAO. We do not yet know how these winter climatic events influence the lynx cycle, but we suggest that lynx hunting efficiency needs to be measured in the three climatic regions.

References and Notes

1. C. S. Elton, *Br. J. Exp. Biol.* **2**, 119 (1924); *Voles, Mice and Lemmings* (Clarendon, Oxford, 1942); see also (3).
2. See P. A. P. Moran [*Aust. J. Zool.* **1**, 163 (1953)], who fitted a linear autoregressive model of order two, which

exhibits quasi-periodicity, but was well aware of its inadequacy. In particular, he pointed out the inhomogeneity of the fitted residuals, which violated the assumption of a common and constant variance for the white noise term in the fitted model. As an interesting historical point, it should be noted that Moran learned about the lynx data when he visited Charles Elton and Dennis Chitty in the Bureau of Animal Population at Oxford after World War II.

3. N. C. Stenseth *et al.* *Proc. Natl. Acad. Sci. U.S.A.* **95**, 15430 (1998).
4. E. Ranta, V. Kaitala, P. Lundberg, *Science* **278**, 1621 (1997); E. Ranta, V. Kaitala, J. Lindström, *Ecography* **20**, 454 (1997).
5. The focus on one particular lynx series has to some extent distracted both ecologists and statisticians up to the present from the fact that similar time series exist for the entire continent [but see T. Royama, *Analytical Population Dynamics* (Chapman and Hall, London, 1992)].
6. K. S. Chan, H. Tong, N. C. Stenseth, unpublished data.
7. C. S. Elton and M. Nicholson, *J. Anim. Ecol.* **11**, 215 (1942).
8. Statistics Canada; Dominion Bureau of Statistics 1965; Statistics Canada 1983–1995.
9. H. Walters, *Vegetation of the Earth and Ecological Systems of the Geobiosphere* (Springer-Verlag, Berlin, 1985); R. G. Bailey, *Ecoregions: The Ecosystem Geography of the Oceans and Continents* (Springer-Verlag, Berlin, 1998).
10. J. W. Hurrell and H. Van Loon, *Clim. Change* **36**, 301 (1997).
11. In principle there are more than 2^{21} classifications of the 21 lynx series. A "black-box" approach means doing an exhaustive search for the optimum combination in some sense—an approach troubled by mul-

tiple comparison in statistical modeling. Instead, we focus on two sets of combinations, one based on ecological features and the other on climatic condition.
12. J. W. Hurrell, *Geophys. Res. Lett.* **23**, 665 (1996).
13. E. Post and N. C. Stenseth, *J. Anim. Ecol.* **67**, 537 (1998); M. C. Forchhammer, N. C. Stenseth, E. Post, R. Langvatn, *Proc. R. Soc. London Ser. B* **265**, 341 (1998); E. Post and N. C. Stenseth, *Ecology* **80**, 1322 (1999).
14. H. Tong, *Non-Linear Time Series: A Dynamical System Approach* (Clarendon Press, Oxford, 1990); H. Tong, *Threshold Models in Non-Linear Time Series Analysis* (Springer-Verlag, Berlin, 1983). The model given by Eq. (1) is a SETAR(2;2,2) model. For a nontechnical presentation of the SETAR models, see Stenseth *et al.* [N. C. Stenseth, K.-S. Chan, E. Framstad, H. Tong, *Proc. R. Soc. London Ser. B* **265**, 1957 (1998)].
15. N. C. Stenseth, W. Falck, O. N. Bjørnstad, C. J. Krebs, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 5147 (1997).
16. N. C. Stenseth and K.-S. Chan, *Nature* **395**, 620 (1998).
17. D. R. Cox and D. V. Hinkley, *Theoretical Statistics* (Chapman & Hall, London, 1974); H. Akaike, in *Second International Symposium on Information Theory*, B. N. Petrov and F. Csaki, Eds. (Akademiai Kiado, Budapest, 1973); H. Akaike, *IEEE Trans. Autom. Cont.* **AC-19**, 716 (1974).
18. Using the tests described in (22) and adopting a 5% significance level, we cannot reject the hypothesis of common slopes and the hypothesis of the common ratio of intercepts for the pairs (L1 and L2) and (L4 and L5). For L6 and L7, we cannot reject the hypothesis of common slopes in the upper regimes and that the lag-2 coefficients may be the same for the two series. However, L6 and L7 appear to have a different lag-1 coefficient in the lower regime. Thus, the evidence of common dynamics for L6 and L7 is somewhat weak. For details, see (6).
19. B. Wiken, D. Gauthier, I. Marshall, K. Lawton, H. Hirvonen, *A Perspective on Canada's Ecosystems*, CCEA Occasional Paper No. 14, Ottawa (1996).
20. J. S. Rowe, *Forest Regions of Canada* (publ. 1300, Environment Canada, Canadian Forestry Service, Ottawa, 1972).
21. We have investigated the constraint structure further (Table 1): assuming only a common structure in the lag-1 and lag-2 in the upper regime provides worse fit. This suggests that the additional constraints [found by testing (6)] are significant. Relocating L3 to the Pacific-maritime group yields an AIC slightly larger than -1819.38. This implies some fuzziness in the boundary of the three zones. One can classify L3 into the Pacific-maritime zone or the Continental zone. The case of Yukon seems rather clear cut: including it in the Pacific zone substantially increases the AIC and hence provides a poorer description.
22. Supplementary information is available at www.sciencemag.org/feature/data/1037845.shl.
23. J. M. Wallace and D. S. Gutzler, *Mon. Weather Rev.* **109**, 784 (1981).
24. Ecosystem Stratification Working Group, *A National Ecological Framework for Canada* (Agriculture and Agri-Food Canada/Environment Canada, Ottawa, 1995).
25. This work was initiated while several of the authors were at the Centre for Advanced Study at the Norwegian Academy for Sciences and Letters, Oslo. N.C.S. acknowledges generous support from the Norwegian Science Council and the University of Oslo. K.-S.C. acknowledges generous support from the University of Iowa. H.T. acknowledges the Engineering and Physical Sciences Research Council (UK) and the University of Hong Kong for support. N.C.S. and H.T. acknowledge support from UK Biotechnology and Biological Sciences Research Council/Engineering and Physical Sciences Research Council (UK) grant 96/MMI09785. R.B., S.B., and C.J.K. acknowledge support from the Natural Sciences and Engineering Research Council of Canada. E.P. acknowledges the National Science Foundation (grant DBI-98-04178) for support. M.C.F. acknowledges the Danish National Research Council for support. We thank A. Kenney for preparing the figure and three anonymous reviewers for providing valuable comments, helping us to clarify our argument.

17 December 1998; accepted 21 June 1999