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Assessing the relative importance of intrinsic and extrinsic influence on sheep population dynamics on Hirta Island, UK

Xiongwen Chen[a,b,*], Bai-Lian Li[a]

[a]*Ecological Complexity and Modeling Laboratory, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124, USA*
[b]*Center for Forestry and Ecology, P.O. Box 1927, Alabama A & M University, Normal, AL 35762, USA*

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Summary

Identifying the relative importance of intrinsic factors and extrinsic environmental variations on population or ecosystem dynamics is important for ecological conservation research. Here, we use a systematic method proposed by De Menezes and Barabási [2004. Separating internal and external dynamics of complex systems. Physical Review Letters, 93, 068701] to reanalyse the long-term monitoring data of Soay sheep population fluctuations and climate variations on Hirta Island, UK. Our results indicate that the climate conditions have a higher impact than internal factors on the fluctuations of sheep population. The sheep population dynamics are internally self-regulating. The scaling relationships between sheep population and external and internal standard deviations are similar. The threshold of the sheep population on this island as determined by our study is around 1197, which is consistent with previous studies by other methods. Our study indicates that this systematic method may help to understand some of the complicated aspects of population dynamics about which detailed knowledge is limited.

Introduction

The relative importance of abiotic versus biotic (both intrinsic and extrinsic factors) influence on species and community dynamics were argued long ago by Clements (1916) and Gleason (1917, 1926). However, this argument is still a major concern in modern ecological and conservation research (Ellner & Turchin, 1995; Leris et al., 1997; May, 1973; Royama, 1992; Sugihara, 1995; Stenseth, Bjornstad, & Saitoh, 1996). The main problem is that we still lack a systematic method to compare the relative importance of external and internal impacts within or across

*Corresponding author. Center for Forestry and Ecology, P.O. Box 1927, Alabama A & M University, Normal, AL 35762, USA. Tel.: +1 256 372 4231; fax: +1 256 372 8404.
E-mail address: xiongwen.chen@email.aamu.edu (X. Chen).

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systems without generating considerable detailed information of mechanisms (Osbenberg & Mittelbach, 1996; Underwood & Petraitis, 1993), although many sophisticated tools are available to asses the impact of environmental variations on system dynamics by analysing time series (Kautz & Schreiber, 1997; Livina et al., 2003; Peng et al., 1994). Currently, the relative importance and potential interaction of internal and external influences on population (or ecosystem) dynamics has important implications for possible ecological consequences of global climate change. Climate change is widely predicted to cause shifts of species and ecosystem distributions (e.g., Crick, Dudley, Glue, & Thomson, 1997; Fraser, Trivelpiece, Ainley, & Trivelpiece, 1992; McCarthy, Canziani, Leary, Dokken, & White, 2001; Root et al., 2003).

De Menezes and Barabási (2004) proposed a general method to separate the importance of internal and external factors in complex systems based on multiple time series from a number of components which interact with each other, and their method was successfully applied to determine the original dynamics in various mechanical systems, such as Internet and computer chip. However, it has not yet been used in ecological systems. Here, we apply this method to sheep population dynamics on Hirta Island in the UK and compare the results with the previous study of Grenfell et al. (1998).

Methods

Study area and time series data

The study area was on the island of Hirta in the St. Kilda archipelago off northwest Scotland. Information on Soay sheep populations and time series of the population and weather conditions were obtained mainly from Grenfell et al. (1998). The sheep population dynamics and its relationship with environmental factors have been intensively studied (Coulson et al., 2000; Coulson, Milner-Gulland, & Clutton-Brock, 2001; Stenseth et al., 2004). We extracted the time series of sheep population and meteorological factors (mean monthly temperature, total monthly precipitation, mean monthly wind speed, number of days with an air frost (air temperature below 0) and number of days with a ground frost (ground temperature below 0)) from 1957 to 1994 in order to be consistent with each other.

Comparing internal and external contribution

The dynamics of the sheep population is attributed to two factors: (i) internal factors, such as competition for food; and (ii) external factors, such as mortality under cold weather. We can separate the two contributions from each component i ($i = 1, \ldots, N$) as the following:

$$f_i(t) = f_i^{\text{int}}(t) + f_i^{\text{ext}}(t). \quad (1)$$

Here, the number of the component N was chosen by available data sets and components which can explain most variances of sheep population (Grenfell et al., 1998). According to the method of De Menezes and Barabási (2004), without detailed knowledge of the system's dynamic rules, we can estimate the ratio of the total fluctuations going through all the observed N components in the time interval $t \in [0, T]$:

$$A_i = \frac{\sum_{t=1}^{T} f_i(t)}{\sum_{t=1}^{T}\sum_{i=1}^{N} f_i(t)}. \quad (2)$$

If only external fluctuations contribute to the activity of node i, at any moment t the amount of fluctuation to go through node i is estimated by the product A_i and the total fluctuation in the system at moment t follows:

$$f_i^{\text{ext}}(t) = A_i \sum_{i=1}^{N} f_i(t), \quad (3)$$

then,

$$f_i^{\text{int}}(t) = f_i(t) - A_i \sum_{i=1}^{N} f_i(t). \quad (4)$$

For each recorded signal I, the external and internal standard deviations (σ_i^{ext} and σ_i^{int}) and their ratio (η_i) can be calculated,

$$\eta_i = \frac{\sigma_i^{\text{ext}}}{\sigma_i^{\text{int}}}. \quad (5)$$

When $\eta_i \gg 1$, the external fluctuation dominate the dynamics of component i, while for $\eta_i \ll 1$ the system's internal dynamics dominates over the externally imposed changes (De Menezes & Barabási, 2004).

Scaling comparison

For each recorded signal the time average $\langle f_i \rangle$ and the standard deviation σ_i from external and internal influences obey the scaling law $\sigma_i \backsim \langle f_i \rangle^{\alpha}$ (De Menezes & Barabási, 2004). De Menezes and Barabási (2004) also indicated that if the internal and external contributions follow the same scaling, the systems' external fluctuations should have a strong impact on the overall dynamics of systems.