

# Estimation of cell numbers

MPN counting was performed as follows. A tenfold dilution series was prepared from sediment samples, using tubes containing a freshwater medium<sup>16</sup> with 20 mM acetate as the electron donor and 56 mM Fe(III)-citrate as the electron acceptor. The tubes were incubated at 20 °C and scored on a weekly basis for the reduction of Fe(III) using the ferrozine assay<sup>16</sup>. The numbers of positive tubes were tabulated and the most probable number of Fe(III)-reducing bacteria estimated by comparison with reference MPN tables.

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# Why large-scale climate indices seem to predict ecological processes better than local weather

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Large-scale climatic indices such as the North Atlantic Oscillation<sup>1</sup> are associated with population dynamics<sup>2</sup>, variation in demographic rates<sup>3</sup> and values of phenotypic traits<sup>4,5</sup> in many species. Paradoxically, these large-scale indices can seem to be better predictors of ecological processes than local climate<sup>5–8</sup>. Using detailed data from a population of Soay sheep<sup>9,10</sup>, we show that high rainfall, high winds or low temperatures at any time during a 3-month period can cause mortality either immediately or lagged by a few days. Most measures of local climate used by ecologists fail to capture such complex associations between weather and ecological process, and this may help to explain why large-scale, seasonal indices of climate spanning several months can outperform local climatic factors. Furthermore, we show why an understanding of the mechanism by which climate influences population ecology is important. Through simulation we demonstrate that the timing of bad weather within a period of mortality can have an important modifying influence on intra-specific competition for food, revealing an interaction between climate and density dependence<sup>11</sup> that the use of large-scale climatic indices or inappropriate local weather variables might obscure.

The impact of climatic variation on ecological processes has been the focus of discussion in ecology for nearly a century<sup>12</sup>. After a period when ecologists believed that complex dynamics were determined primarily by density-dependent intrinsic processes<sup>13</sup>, recent work has shown that climatic variation can have an important role—either directly or through its interaction with density<sup>14,15</sup>. It has emerged that large-scale seasonal indices of climate, such as the North Atlantic Oscillation (NAO, defined as fluctuations in sea-level air pressure between the Atlantic sub-polar low-pressure zone centred around Iceland and the sub-tropic high-pressure zone centred around the Azores<sup>1</sup>), are remarkably good predictors of ecological variation—often better than local weather variables<sup>4–6,16–18</sup> (but see refs 19–22 for examples where local weather predicts ecological processes well). The strong performance of large-scale climatic indices in predicting ecological processes is often difficult to reconcile with the proximal physiological processes that underpin them<sup>10</sup>. For example, in the food-limited population of Soay sheep (*Ovis aries*) considered here, there are two mechanisms by which winter weather influences mortality rates: first, by generating energetic costs on animals in poor condition, and second, by moderating vegetation productivity and available grazing for sheep during winter<sup>14,23,24</sup>. In this system one may therefore expect short-term local climatic averages to predict mortality rates better than large-scale indices estimated over multiple months, yet some studies<sup>3,6,25</sup> found that the NAO predicted mortality rates better than indexes of local monthly weather and explained approximately 20–30% of the variation in mortality. These results have presumably

arisen because the local climate measures used—typically average monthly temperature or rainfall—do not adequately capture the climatic conditions that influence sheep demographic rates<sup>7,8</sup>. Identifying how climatic variables influence demographic rates in wild populations is, however, critical if the relative roles of density and climate are to be identified accurately. The challenge facing ecologists is to identify the appropriate climatic variables to use<sup>7,8</sup>.

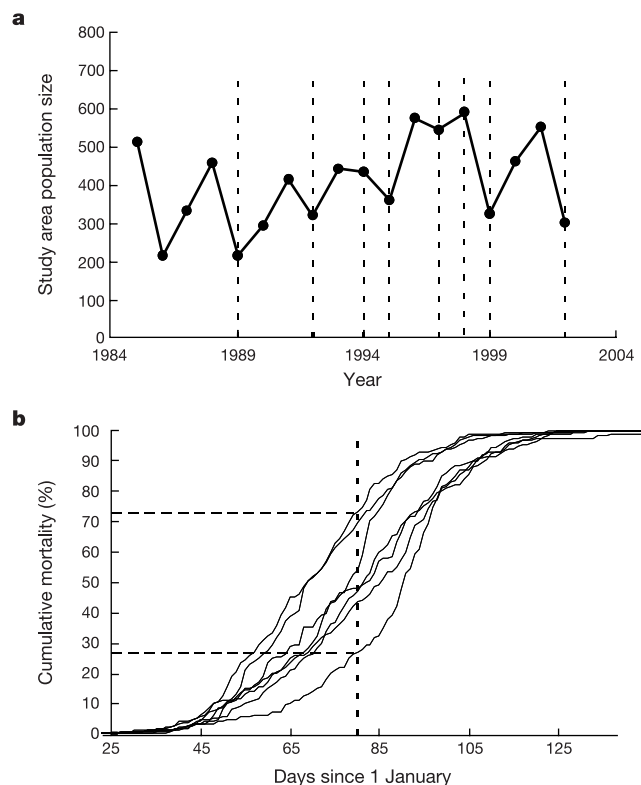
The Soay sheep population living in the Village Bay catchment of Hirta in the St Kilda archipelago has been the focus of a detailed, long-term, individual-based study since 1985 (ref. 10). During winter, daily mortality searches of the study area are conducted providing unusually detailed death-date data, accurate to a day for 83.3% of animals that are known to have died, for individuals born into the 1986–2002 cohorts. Daily weather data were collected by the meteorological office at Stornoway, an island approximately 100 km from St Kilda. From these data, the weekly total rainfall, and weekly averages of the maximum gust speed and minimum air temperature, were calculated. Comparison with local weather measurements on Hirta during the winters of 2000–02 indicates that the Stornoway data capture local conditions closely (temperature,  $r = 0.92$ ; gust speed,  $r = 0.82$ ; rainfall,  $r = 0.78$ ). These demographic and climate data provide us with an opportunity to examine the link between climate and mortality in unprecedented detail.

Our aim is to identify climatic conditions associated with death in this system. We do this by restricting our analyses to mortality occurring in the 8 yr when the death date of more than 100 individuals is known, thus providing us with sufficiently large sample sizes to allow robust statistical analysis. Consequently we

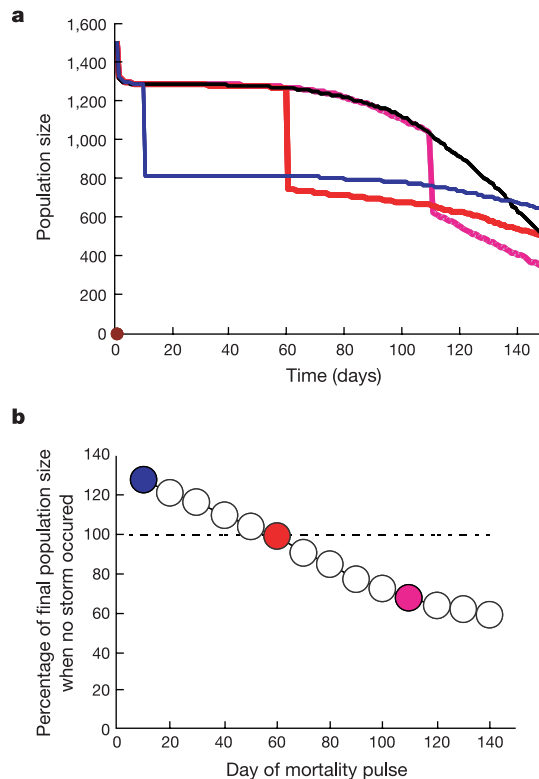
concentrate on mortality in 1989 ( $N = 227$ ), 1992 ( $N = 213$ ), 1994 ( $N = 125$ ), 1995 ( $N = 160$ ), 1997 ( $N = 180$ ), 1998 ( $N = 110$ ), 1999 ( $N = 393$ ) and 2002 ( $N = 344$ ) (Fig. 1a). Although more than 150 animals died in each of these years (including those with less precise death dates) the overall mortality rate this represents ranges from 28% to 68% (Fig. 1a).

We divide the mortality records by sex and age (classified as lambs, yearlings and adults). The association between local weather and mortality was investigated by regressing weekly death counts against weekly weather variables (see Methods). To account for the possible delay in the effect of weather on mortality, we also regressed weekly death counts against weekly weather variables from one and two weeks previously. Detailed data on weights of animals in summer and on gut parasite load (approximated from faecal egg counts) exist for many individuals within this population<sup>26</sup> but inclusion of these terms in models did not alter our general conclusions: heavier individuals die later than lighter ones<sup>27</sup> and parasite-laden individuals die earlier than those that are relatively free of parasites<sup>28</sup>, but weather in the weeks before death is still associated with mortality. We do not report these analyses in detail below as they diminish the sample size available to us within each year (as not all animals are caught) and the number of years available for comparison.

The timing of the pulses of mortality varies greatly between years (Fig. 1b). In each year most mortality occurs within the first 18 weeks (January to early May) but within this period the amount of death in each month varies considerably: the percentage of the total number of sheep dying in February, March and April ranges between 6–24%, 35–66% and 9–50%, respectively. The variation



**Figure 1** Dynamics of Soay sheep. **a**, Variation in study area population size between 1985 and 2002. Dotted vertical lines identify the years chosen for analysis. There were too few animals with exact death dates known to allow analysis of the 1986 population crash. **b**, Variation in the timing of mortality in different years. Each line represents the cumulative percentage mortality per day since 1 January. The vertical dotted line highlights differences in the cumulative proportion dead by 21 March, whereas the horizontal lines allow ease of reading (upper horizontal line is at 73% (1999), lower horizontal line at 27% (1994)).



**Figure 2** Results from the simulation model. **a**, Effects on population size of altering the timing of the pulse of mortality. The black line indicates the population size in the absence of a storm. The earlier the pulse is in the year (blue line, pulse at day 10; red line, pulse at day 60; purple line, pulse at day 110) the more animals survive the winter. **b**, Simulated final population size after mortality pulses as a percentage of the final population size when no pulse occurs. A pulse of mortality early in winter can generate a larger final population size than a simulation without such a pulse (dashed line). Coloured points identify simulations displayed in **a**.

in the timing of mortality helps to explain why local climatic variables calculated over a fixed 1-month time period that have previously been used<sup>28</sup> fail to predict inter-annual variation in overall mortality rates as well as the NAO. Despite variation in the timing of mortality, the overall structure of the pulse of mortality is the same in all years: males and lambs of either sex die earlier than female yearlings and female adults. The comparative lateness of female yearling and female adult mortality explains why previous research has found that February and March rainfalls are significantly associated with mortality rates in these two demographic classes.

The association between each weather variable and the timing of death varies greatly between years (Table 1). In one year a local weather variable can explain substantial amounts of variation in the timing of death, whereas in another year it can be uncorrelated with the timing of death. For example, air temperature is negatively linked to the timing of death in 2002 for almost all groups of sheep, but is largely uncorrelated with the timing of deaths in 1989 and 1997, with which rainfall and gust speed are closely associated (Table 1).

These results provide a demonstration of how the NAO can outperform local previously used weather variables<sup>3,6,25</sup> in predicting ecological processes. The structure of pulses of death in each year is consistent with death by starvation (the major cause of death of sheep on Hirta<sup>28</sup>) resulting from an individual's energy deficit

caused either by the energetic cost of thermoregulation or the diminished availability of forage in bad winter weather<sup>23,24</sup>. The inter-annual variation in the timing of the pulses of death indicates that such conditions can occur at any time during the period from February to April (Fig. 1b). The variation in the association between each local weather variable and the timing of death (Table 1) indicates that energetically demanding conditions can occur in any form: heavy rainfall, strong wind or cold temperatures. This complex association is compounded further by the delay between these conditions occurring and the increase in mortality they cause (Table 1). Energetically challenging conditions can therefore occur at different times and in different forms in each year, and their effects may be expressed immediately or after a delay of one or two weeks. Thus, a variable in which a time and a type of energetically challenging condition is specified (for example, March rainfall) will in some years fail to capture the event that causes death. The NAO, by contrast, is a multi-month average that holds information on rainfall, wind speed and temperature<sup>1</sup> and thus serves as a 'catch-all' for energetically challenging conditions of any kind at any time in winter.

Local weather will, of course, always be a more powerful determinant of the timing of sheep death as long as the mechanism by which it affects ecological processes can be captured in a variable. Different components of local weather may be associated with an

Table 1 Associations between weather variables and mortality in years when substantial mortality occurred

Variable	1989			1992			1994			1995		
	W	W - 1	W - 2	W	W - 1	W - 2	W	W - 1	W - 2	W	W - 1	W - 2
<b>Air temperature</b>												
Male lamb	—	24%	23%	<b>35%</b>	—	—	—	—	25%	21%	29%	30%
Female lamb	—	28%	—	—	—	—	—	—	—	—	—	—
Male yearling	—	—	—	<b>41%</b>	—	—	—	49%	—	—	—	—
Female yearling	—	—	—	—	—	<b>43%</b>	51%	—	52%	—	—	—
Male adult	—	—	—	<b>43%</b>	<b>40%</b>	—	—	—	—	—	—	26%
Female adult	—	—	—	—	—	<b>31%</b>	—	—	—	—	—	—
<b>Rainfall</b>												
Male lamb	—	<b>25%</b>	<b>35%</b>	26%	31%	38%	—	—	—	—	—	—
Female lamb	<b>30%</b>	<b>25%</b>	—	—	—	—	—	—	—	—	—	—
Male yearling	<b>34%</b>	<b>34%</b>	—	—	—	—	—	—	—	—	47%	—
Female yearling	—	—	—	—	—	—	—	—	53%	38%	—	—
Male adult	—	<b>37%</b>	—	68%	22%	—	—	—	—	—	—	—
Female adult	—	<b>20%</b>	<b>27%</b>	—	—	—	—	—	—	—	—	—
<b>Gust speed</b>												
Male lamb	—	22%	—	—	27%	—	—	24%	—	—	—	—
Female lamb	—	32%	—	—	—	—	—	—	—	—	—	—
Male yearling	—	—	26%	—	—	—	—	—	—	—	<b>65%</b>	<b>28%</b>
Female yearling	—	—	—	—	—	—	55%	72%	44%	—	—	—
Male adult	—	—	38%	—	23%	—	—	—	—	<b>25%</b>	<b>25%</b>	<b>41%</b>
<b>Variable</b>												
<b>1997</b>												
<b>1998</b>												
<b>1999</b>												
<b>2002</b>												
<b>Air temperature</b>												
Male lamb	—	—	—	—	—	—	<b>35%</b>	<b>30%</b>	<b>26%</b>	<b>67%</b>	<b>44%</b>	<b>47%</b>
Female lamb	—	—	—	—	—	—	—	—	<b>26%</b>	<b>49%</b>	<b>65%</b>	<b>49%</b>
Male yearling	—	—	—	—	—	—	<b>53%</b>	<b>23%</b>	<b>73%</b>	—	<b>26%</b>	<b>63%</b>
Female yearling	—	—	—	—	No data	—	—	—	—	—	—	—
Male adult	22%	—	50%	28%	—	28%	—	—	<b>58%</b>	<b>28%</b>	<b>31%</b>	<b>69%</b>
Female adult	—	—	—	—	—	—	—	—	—	—	—	—
<b>Rainfall</b>												
Male lamb	—	—	—	—	—	32%	—	—	21%	56%	—	—
Female lamb	—	—	—	—	—	—	—	23%	—	—	—	—
Male yearling	—	—	—	—	—	—	—	—	29%	—	—	36%
Female yearling	—	—	—	—	No data	—	—	—	—	22%	—	—
Male adult	70%	—	—	—	—	—	—	—	—	27%	—	34%
Female adult	—	—	—	—	—	—	36%	—	—	—	23%	—
<b>Gust speed</b>												
Male lamb	—	—	<b>23%</b>	—	22%	—	28%	—	—	25%	—	—
Female lamb	—	—	—	—	—	—	—	—	—	—	—	—
Male yearling	—	<b>22%</b>	—	—	—	—	39%	41%	—	—	—	—
Female yearling	<b>59%</b>	—	—	—	No data	—	—	—	—	—	—	—
Male adult	—	<b>59%</b>	—	—	—	—	—	24%	—	36%	—	—
Female adult	—	<b>31%</b>	—	—	—	—	—	—	—	—	—	—

Associations with weather during the week of mortality (w) and one (w - 1) and two weeks (w - 2) before mortality are reported. Values represent the percentage of variation explained in the timing of mortality for each age group. Terms that explain more than 20% of the variation are reported; all values produce significant *P*-values following Bonferroni correction. Values in years when mortality rates in most age and sex classes were explained well by one type of weather are in bold.

ecological process in multiple ways, making the choice of a local weather variable non-trivial. Furthermore, different local ecological processes are likely to be associated with a range of local weather variables. The challenge for ecologists is to identify sensible statistics to describe the multivariate and spatially heterogeneous time series that constitute local weather. This challenge is only likely to be met if the mechanism by which climate influences ecology is known. The paradoxical performance of large-scale weather variables such as the NAO must simply reflect the low accuracy with which the biological consequences of local weather are captured with the local weather variables typically used by ecologists. In fact, for the Soay sheep system, the NAO also codes the severity of winter weather inefficiently: both high and low NAO values can reflect energetically challenging conditions<sup>1</sup>. We expect, therefore, that detailed local weather data could be compiled into a new seasonal index that would outperform the NAO in predicting winter mortality rates.

In the Soay sheep system there are various factors that might influence mortality: the timing of a spell of bad weather, as well as previous weather in the winter. If a storm in one week killed all animals that were in poor condition an even stronger storm the following week would have little or no impact on mortality. Consequently any local measure of climate should not only incorporate multiple weather types (temperature, precipitation, wind speed) over a long period, but should also incorporate the effects of any harsh weather earlier in the season in either removing weak animals from the population or in weakening animals in better condition. Until the influence of climate can be understood in sufficient detail, the relative influence of climate and density dependence on ecological processes and the consequences of global climate change cannot adequately be appreciated. Development of a local, integrative climatic index is beyond the scope of this paper. However, we do theoretically explore how the timing of a bout of mortality could markedly modify the number of individuals that die in a year in a resource-limited population, similar to the Soay sheep system.

We constructed a simulation model of an overwintering population with a limited amount of food (see Methods). Density-dependent mortality is assumed to result from the daily intraspecific competition for food, and the chance of any individual dying is related to the amount of food it has recently consumed. Density-independent mortality is included in the form of a pulse of death (as would result from a spell of bad weather) whereby on one day each individual is exposed to an additional chance of dying. These minimal assumptions allow the results to be generalized; a consequence of this is that the model will not necessarily be a perfect caricature of any specific system, as factors such as demographic structure and day-to-day variation in energetic costs are not included in the simulation.

The later the pulse of mortality occurs, the lower the final population size (Fig. 2). This extends to the counter-intuitive result that a population that experiences an early death pulse can actually be greater in size at the end of winter than a population that does not experience any pulse (Fig. 2). The pulse of mortality, in reducing the population size, increases the chance of the remaining individuals surviving to the end of winter. This effect is enhanced when the pulse occurs earlier rather than later, as there is more food available for survivors—the victims of the death pulse having stopped eating sooner (Fig. 2). The model demonstrates that a density-dependent process can modify the strength of a density-independent process. We suggest that such time-dependent interactions may limit the power of the NAO and other crude climatic summaries in predicting ecological processes, and that a complete analysis of climatic effects in ecology cannot be limited to such data.

The ability of the NAO to outperform proxies of local climatic conditions in explaining variation in ecological processes has repeatedly been demonstrated<sup>4–6,16–18</sup> and seemed paradoxical given the mechanisms by which climatic variation imposes ener-

getic stresses and influences resource availability in the wild. Our results verify that one explanation of this paradox<sup>7,8</sup> may be the complicated and temporally variable associations between local climate and ecological process, which monthly climatic averages fail to capture but which the NAO can incompletely reflect. Although very few studies of free-living populations have detailed data on the timing of mortality, there is no reason to expect that these complex patterns are specific to the Soay sheep. Our results therefore provide biological justification for the inclusion of large-scale climate indices in analyses of ecological processes rather than crude summaries of local climatic conditions. However, we also stress that a detailed understanding of climate–ecology interactions can only come from synthesis of detailed data on local weather and mortality and, if possible, identification of the mechanisms by which climatic effects are expressed. □

## Methods

### Data

Sheep are sexed and uniquely marked within hours of birth, allowing age to be known accurately. Daily searches of the study area are conducted during winter when mortality occurs. Weather data are collected from the meteorological office at Stornoway and are available at <http://badc.nerc.ac.uk/home/>. We used data on daily precipitation (in millimetres to the nearest 0.2 mm), maximum gust speed ( $\text{m s}^{-1}$ ) 2.25 m above ground and minimum ambient air temperature at 1.5 m ( $^{\circ}\text{C}$ ).

### Statistical methods

For each year analysed the week-of-death of every individual was calculated (on the basis that week 1 included death dates from 1 January to 7 January inclusive, and so on). A frequency distribution of deaths over the first 18 weeks was then calculated for male lambs (<1 yr of age), female lambs, male yearlings (>1 and <2 yr of age), female yearlings, male adults and female adults. Within-year sample sizes were not sufficient to separate male and female adults into the prime-aged and older adults age classes that have been used previously for examination of survival rates between years. Weekly climate variables were regressed against the number of deaths per week, the number of deaths the following week and the number of deaths 2 weeks later. This approach does not allow an explicit description of the 'killing power' of each weather element but does provide an estimate of the weather element with which the timing of death of those that succumb was most associated.

### Simulation model

The simulation model follows the fate of  $N$  individuals through  $T$  winter days with a finite amount of food,  $F$ . Before the first day the population is divided equally among five energetic states (1–5) and the energetic class of the  $i$ th individual is denoted  $c_i$ . Population size at time  $t$  is denoted  $N_t$ . On each day the probability of each individual finding food is evaluated from a function  $p(F_t, N_t)$ , where  $F_t$  is the food currently available. In Fig. 2,  $p(F_t, N_t) = \{1 - \exp(-aF_t)\} / \{1 + \exp(-b(N_t - N_0))\}$ , where  $a$  and  $b$  are model coefficients; all functions we tried that increase monotonically over positive values of  $F_t$  and decrease monotonically over positive values of  $N_t$  produced similar results. If an individual finds food its energetic state ( $c_i$ ) is increased by one; if it fails to find food its energetic state is decreased by one. If an animal in the lowest energetic state ( $c_i = 1$ ) fails to find food it dies. The total amount of food available to the population is updated every day. The initial amount of food available is insufficient to feed each member of the initial population on every day of the simulation (that is,  $F < NT$ ). On one day all individuals are exposed to an additional chance of dying that depends on their state on that day,  $p(c_i)$ . In Fig. 2,  $p(c_i) = p_{\max} \exp[\beta(c_i - 1)]$ , where  $p_{\max}$  ( $0 < p_{\max} \leq 1$ ) is the chance of an animal of the lowest energetic state ( $c_i = 1$ ) dying.

Our key assumptions are that the chance of obtaining food each day depends on the current population size and the amount of food available, and that there is insufficient food to feed each member of the initial population every day. The energetic state of each individual determines its chance of dying (through both starvation and the death pulse) and this state is modified by the amount of food that has recently been consumed. The values of the parameters discussed alter the strength but not the qualitative nature of our results: in Fig. 2  $N_0 = 1,500$ ,  $T = 150$ ,  $F_0 = 2.10^5$ ,  $a = 10^{-5}$ ,  $b = 0.2$ ,  $\beta = 0.06$  and  $p_{\max} = 0.5$ .

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## Microbialite resurgence after the Late Ordovician extinction

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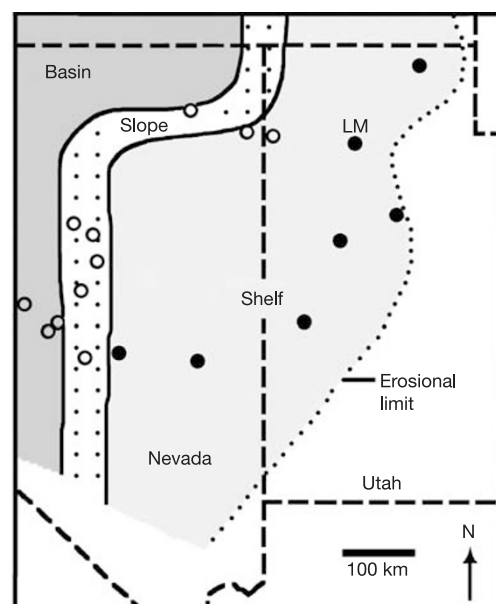
Microbialites, including biogenic stromatolites, thrombolites and dendrolites, were formed by various microbial mats that trapped and bound sediments or formed the locus of mineral precipitation<sup>1</sup>. Microbialites were common and diverse during the Proterozoic<sup>2–4</sup>, but declined in abundance and morphological diversity when multicellular life diversified during the Cambrian

Radiation. A second decline occurred during the Ordovician Radiation of marine animals, and from then until the present microbialites have been confined largely to high-stress environments where multicellular organisms are rare. The microbialite declines in the Phanerozoic are attributed to disruption of the mats by animals<sup>2,5,6</sup>. A resurgence of stromatolite abundance and size during reduced animal diversity after the Permian extinction<sup>7</sup> has been documented anecdotally. Here we show, with statistical support, that a microbialite resurgence also occurred after the Late Ordovician extinction event in western North America. The resurgences were associated with loss of mat-inhibiting animals, providing insights into shallow-water community structures after extinction events.

We document three aspects of microbialite resurgence that followed the Late Ordovician extinction event (LOEE) using centimetre-scale sedimentological logs of carbonate rocks deposited on the shelf margin of the western USA. First, microbialites increased in size and abundance. Second, morphological diversity increased as thrombolites and columnar stromatolites appeared in abundance for the first time since the Ordovician Radiation; these earliest Silurian microbialites resemble those of the Cambrian and early Ordovician, before the macrofauna expanded during the Ordovician Radiation. Third, the microbialite resurgence, which lasted roughly 5 million years (Myr), corresponds with widespread, low-diversity megafaunal communities of the post-extinction recovery interval.

One of the most extensive tropical carbonate platforms known in the world during the Late Ordovician and Early Silurian is preserved in the eastern Great Basin. The westward-deepening carbonate platform (Fig. 1) has five upper Ordovician ramp sequences (O1–O5), and three lower-middle Silurian ramp sequences (S1–S3), followed by three rimmed-shelf sequences (S4–S6)<sup>8,9</sup>. The faunas and ecological patterns have been documented<sup>10,11</sup> and tied to a sequence stratigraphic framework.

Sequence O5 was deposited during an interval of glacio-eustatic sea-level draw-down associated with the LOEE, one of the five great Phanerozoic extinction events<sup>12</sup>. The LOEE was caused by the brief (~0.5 Myr) Hirnantian glaciation that produced climatic changes



**Figure 1** Palaeogeographic map of lowest Silurian (sequence S1). Circles indicate measured sections; filled circles indicate the occurrence of at least one bed with microbial domes. LM, Lakeside Mountains locality.