



Figure 2 The distribution of positrons near the centre of our Galaxy, obtained with OSSE. The brightest feature is the Galactic nucleus, and the horizontal structure lies along the Milky Way. The newly discovered antimatter cloud, or 'fountain', is above the centre.

particle acceleration, and physical processes near compact objects.

By imaging nuclear-decay γ -rays from radioactive isotopes such as ^{26}Al and ^{44}Ti , we can now see directly where in our Galaxy new elements are being formed and mixed into the interstellar medium by massive stars and supernovae (Fig. 1). Furthermore, we can witness nuclear interactions through nuclear de-excitation lines from, for instance, ^{12}C and ^{16}O . Potential production sites are in violent interstellar environments and near accreting compact objects. Evidence for these spectral features (well known from solar flares) is observed in emission from the nearest site of massive-star formation in giant molecular clouds, the Orion complex, and can now be seen in the large-scale γ -ray glow from the Milky Way as well.

OSSE caused recent excitement in this field. For the past 25 years, more than a dozen balloon and satellite experiments have seen 511-keV emission from the general direction of the Galactic Centre, due to the annihilation of positrons with electrons. Instruments with large fields of view seemed to detect the strongest signal, indicating the presence of more than a single point source. Soon after the launch of the Compton Observatory, OSSE showed that the emission region is indeed extended. An intense glow from the nucleus was seen, with some extension along the Milky Way. But now OSSE has found a new feature (W. R. Purcell, Northwestern Univ.): strong 511-keV emission extends up to 10° above the Galactic Centre (Fig. 2). A 'fountain' of hot gas laden with electron-positron pairs may be rising from the nucleus (C. D. Dermer and J. G. Skibo, Naval Research Lab.), with positrons losing energy and annihilating as they are convected upwards with the gas.

A recent starburst episode near the Galactic Centre could be driving the fountain. And the positrons may come from radioactive material freshly synthesized in stellar explosions associated with the same star-forming activity. The signature of ^{26}Al , for example, might be detectable by future instruments. But nuclear interactions and jets from black holes could also contribute to the positron production.

On the other hand, the enhanced emission may not be related to the nucleus, but instead betray a closer, localized site of positron production and annihilation. If that is the case, other, similar sites may be seen in forthcoming observations.

The Compton Observatory has put γ radiation into the mainstream of astronomy, and it should still solve some of the questions it has raised — after a re-boost into higher orbit was completed on 3 June it is ready for maybe another decade of observations. But more sensitive instruments are needed for radical progress. A new, ten-times-better Compton

Observatory, covering again the low-to-high-energy γ -ray regime, would be colossal, and so is not a realistic option. So a difficult choice must be made: an imaging MeV spectrometer is highly desirable, but so is a telescope to map the high-energy γ -ray sky. As an important next step, the European Space Agency's forthcoming INTEGRAL mission (scheduled for launch in 2001) will drastically improve on spatial and spectral resolution with good sensitivity up to a few MeV. □

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Ecology

Insect pollinators see the light

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The complexity of woodland microclimates has long been a source of fascination for ecologists. The patterns of light on a forest floor produce a constantly changing mosaic of intensities that result in marked — and sometimes rapid — changes in temperature and humidity. These factors contribute to a rich and varying assemblage of microhabitats for plants, animals and microbes, and it is easy to understand how such complexity can support a great diversity of species, especially in the stratified architecture of tropical rainforests. But the degree to which microclimatic complexity influences the interactions between organisms and, in the longer term, coevolution, may not be adequately appreciated.

In a recent issue of *Oikos*, Carlos Herrera¹ has examined the forest-floor irradiance mosaics in open oak/pine woodlands in southern Spain. He has found that the patches of sun and shade are important in determining patterns of pollination for ground-dwelling plants and also, perhaps, for the evolutionary development of the plants themselves.

Plant ecologists have recognized the physiological significance of patchiness in woodland light-climates, particularly in determining the intensity and duration of the solar energy that is available for photosynthesis. Sun flecks — direct patches of sunlight that penetrate gaps in the canopy and strike the forest floor — have been examined in relation to the photosynthetic patterns of low-lying leaves. The overall energy that is supplied by sun flecks has been estimated to account for 10–40 per cent of the forest floor's total energy budget^{2,3}. The variation between habitats was thought to be due to such factors as latitude (angle of the Sun), canopy architecture (tree density, height and stratification), wind and cloud cover. But the sudden arrival of a high-intensity patch of light on a plant that is accustomed to life in deep shade can prove damaging, and some

plants, such as the wood sorrells (*Oxalis* spp.), respond by rapidly lowering their leaves into a vertical position.

Insects are also sensitive to variations in woodland microclimate, both in space and time. Patterns of light intensity can be particularly important in the selection of flowers by pollinators⁴. Pollinator choice may, in fact, be more dependent on the microhabitat of the individual plant than on more obvious influences such as the supply of nectar available. Is this simply a matter of energetics? Do some pollinators prefer to work at gathering food in high-energy, sunlit spots, while others prefer low-energy locations with lower temperatures and higher humidity? If so, could this selection be a consequence of the differing thermal biology of the individual pollinator species?

To answer these questions, Herrera¹ has studied the pollination biology of lavender (*Lavandula latifolia*) in the understorey of open woodland of evergreen oak (*Quercus rotundifolia*) and pine (*Pinus nigra*) in southern Spain. Within this patchy habitat, he established a transect of 60 stations at which irradiance was measured over several consecutive days. In the more shaded areas of the woodland understorey, irradiance levels were generally below 200 W m^{-2} and they rarely exceeded $1,000 \text{ W m}^{-2}$. By contrast, the more open sites spent about 25 per cent of the time at light intensities greater than $1,000 \text{ W m}^{-2}$.

Insect pollinators visiting the lavender were netted throughout the day, and their thoracic temperature was recorded within five seconds of capture, using a needle microprobe. Concentrating on the hymenopterans (bees) and the dipterans (flies), Herrera found that there are strong links between species and habitat conditions. Two of the fly species, for example, foraged only in shaded conditions ($<130 \text{ W m}^{-2}$), whereas two of the bee species were found only under conditions of high irradiation ($>800 \text{ W m}^{-2}$). In general, the flies were

restricted to the more shady environments.

Pollinator species varied considerably in their thoracic temperatures: mean values for different species ranged from 27 °C to 43 °C, with the hymenopterans having consistently higher thoracic temperatures than the dipterans. Similarly, the excess temperature of the thorax over the air temperature at the point of capture was greater in the hymenopterans — often greater than 15 °C, compared with less than 10 °C for the dipterans. Herrera also found that the tendency to generate a thoracic temperature that is greater than that of ambient air is positively correlated with body size, because the processes of warming up and cooling down are related to body form and mass. The conclusion is that the sun-seekers are generally smaller and maintain lower thoracic temperatures than the shade-preferring taxa, which are larger and can keep their body temperatures well above their surroundings. So, the thermal biology of insect species determines what microhabitat they select for their foraging activities. This means that a plant species such as lavender, which can grow and flower both in shaded and open-sun conditions, attracts a different set of pollinators depending on the microclimate of its habitat: a lavender plant in a sunny spot will be visited mainly by small bees, whereas lavender in the shade will attract more dipterans and larger bees.

The biological and evolutionary implications of these findings are considerable. Various insects will have different seasonal abundances, pollination behaviour, efficiency in pollen collection and delivery, and distances over which they travel between plants. All of these factors will present the host plant with a number of selective pressures to which, over

evolutionary time, it will respond. And because these pressures will differ between 'sun' and 'shade' populations of the plant, pollination could be an important influence on the course of evolutionary development. Previously, the existence of sun and shade ecotypes (or even closely related species) of plants has usually been explained in terms of their photosynthetic physiology, including energy trapping and their ability to maintain a positive carbon balance under different light

climates⁵. But the new study by Herrera¹ shows that botanists cannot afford to neglect the energetic properties and predilections of the insect visitors in the process of speciation. □

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1. Herrera, C. M. *Oikos* **78**, 601–611 (1997).
2. Evans, G. C. *J. Ecol.* **44**, 391–428 (1956).
3. Anderson, M. C. *Biol. Rev.* **39**, 425–485 (1964).
4. Herrera, C. M. *Ecology* **76**, 1516–1524 (1995).
5. Bjorkman, O. *Physiol. Planta* **21**, 84–89 (1968).

Demography

Taking the measure of uncertainty

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Judged on performance, population forecasts (usually published by institutions such as the United Nations or census bureaux) have a mixed record. They are no worse than forecasts by economists, meteorologists and others who have to deal with complex and partially understood systems, but demographers have been understandably concerned about error in their predictions. Part of their response is a new wave of demographic work focused on the forecasting of uncertainty, *per se*. Such work aims to forecast a range of demographic outcomes along with associated probabilities, rather than one prediction that will almost surely be wrong.

This new approach is illustrated by Lutz, Sanderson and Scherbov (page 803 of this issue¹), who present a forecast of world population through the year 2050 and up to 2100. They conclude that the odds of world population doubling by 2050 are less than a third, whereas a doubling of the fraction of the population that is over the age of 60 is essentially a sure thing. Their results stem from a consensus of expert opinion that human fertility will continue to fall everywhere, trailing the decline of mortality by about a half-century. Their result is also noteworthy for its assignment of explicit probabilities to alternative futures.

Traditional forecasts use a 'high–medium–low' method, making a central forecast bracketed by two variants. Although the range between 'high' and 'low' indicates uncertainty, no probabilities are associated with the alternative outcomes, so it is difficult to interpret, employ and evaluate them². In contrast, a probabilistic forecast is valuable to anyone who must make a decision that turns on future events, because one may compute the odds of happy and nasty outcomes, and turn decisions into informed gambles. This is no radical idea; investors, for example, routinely use estimated uncertainty to shape their decisions³. But the idea is new to demography, for there are technical challenges, and the forecaster has to educate the people who actually use the forecasts.

A forecaster begins with today's known

conditions and projects to a future date that is characterized by unknown demographic conditions such as the level of fertility or mortality. The expert makes assertions about demographic characteristics (for example the level of fertility or the expected length of life) at the end-point, and the trajectories along which those characteristics will change between start and end. I refer to the first of these as 'static' scenarios, because they describe possible conditions at a single future time, and to the second as 'dynamic' scenarios. Finally, one must attach *a priori* probabilities to each static or dynamic scenario.

Lutz *et al.* establish static scenarios, alternative conditions of fertility and mortality in 2050, with attached probabilities. To make a forecast, select one final fertility and mortality ('there'), specify a time-course along which the starting fertility and mortality ('here') changes to 'there', and project the starting population over that time-course. Repeat for each ending scenario, and weight the projected population by the probability associated with the ending scenario. Astute readers will ask how probabilities are assigned to scenarios, and how one gets to each 'there' from 'here'? Lutz *et al.* employ subjective probabilities based on a sampling of expert opinion; this is a version of what used to be called (with some chutzpah) the Delphi method. A more systematic approach uses a retrospective analysis of expert predictions to quantify their bias and error^{4,5}, and is more objective about assigning probabilities.

The dynamics of getting 'there' from 'here' are largely ignored in the static approach (it is usual to pick some smooth trajectory between initial and final conditions). The usual reasons are a lack of information or a belief that it isn't really important. Neither is convincing in a probabilistic forecast that is motivated precisely by uncertainty.

In contrast, dynamic forecasts employ a stochastic model of changes in fertility, mortality and migration, typically fitted to historical data. The resulting models have uncertainty embedded within them, as reflected in historical change, and yield



Figure 1 When sunny gets blue — plants such as lavender, which can grow and flower in both sunny and shaded areas, are visited by different insect pollinators depending on light intensity. According to Herrera¹, whereas large insects such as flies visit plants in shaded areas, smaller insects preferentially visit plants in sunny spots.

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