

閱讀以下段落後，用中文寫出有關生物學知識的大意(不超過 300 字，切勿逐字翻譯)

1. (20%)

When plants evolved a vascular system containing cells that facilitate the transport of water and nutrients, this not only allowed them to conquer land, but also provided the structural stability that enabled them to increase dramatically in stature, bulk and complexity. The cells that give rise to vascular tissue are specified in the embryo, but in many flowering plants they undergo substantial rounds of proliferation only during post-embryonic development, in a process that drives radial growth and expands the circumference of roots and shoots. This radial growth depends on the division of stem cells located in an inner cylindrical layer of cells called the cambium, which gives rise to wood and the woody fibre used for textiles, called bast.

It has been estimated that woody plant material (arising from cambial cells) accounts for more than half of Earth's biomass. Yet despite the importance of the cambium, our level of understanding about cambial stem cells and their regulation lags behind our knowledge of stem cells in the plant root or shoot tips, probably because the cambium is more difficult to access, given its location in the interior of fully differentiated organs. Writing in *Nature*, Miyashima et al. and Smetana et al. offer insights into cambium development on the basis of studies of roots of the model plant *Arabidopsis thaliana*.

Plant vascular tissue is comprised of water-transporting xylem cells and nutrient-transporting phloem cells, both of which are typically located in a central region of the mature root and stem. These specialized cell types can be separated by the cambium, which is home to dividing cells that drive the expansion of the xylem (which forms wood) and the phloem (which forms bast)<sup>5</sup>. Through an analysis of plants containing mutations in certain genes, and the use of imaging techniques to track fluorescently tagged proteins, Miyashima and colleagues reveal the mechanisms whereby the cell types generated by root-tip stem cells make up the cell layers from which the cambium will form. They show that cambial precursor cells, also known as procambium cells, are specified by a complex molecular network of plant hormones, transcription-factor proteins and microRNAs.

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Miyashima et al. report that, during an initial growth phase that precedes radial expansion, certain phloem cells at the periphery of the vascular tissue act as 'organizers' — cells that promote the division of nearby cells; in this case, the procambial cells. Miyashima and colleagues show that a type of developing phloem cell called a protophloem-sieve-element precursor responds to the hormone cytokinin by expressing proteins of a family of transcription factors that the authors term PEAR proteins. PEAR proteins were also found in the neighbouring developing procambial cells, and the authors suggest that they reached this location from protophloem-sieve-element precursors through a cell-to-cell transport mechanism.

The presence of PEAR proteins can give cells the ability to divide; however, such division competency is limited to cells at the periphery of the vascular tissue. The authors report that this is because, towards the root interior, the hormone auxin, aided by PEAR proteins, causes HD ZIP III transcription factors to accumulate, inhibiting PEAR function. This combination of mobile and non-mobile components enables a dynamic yet robust spatial patterning of cell fate, and lays down the cellular foundation for the establishment of the cambium during the initial phase of the process leading to radial growth.

Focusing on later stages of root thickening, Smetana and colleagues analysed how root procambial cells, which are kept in a dormant state, develop to form the actively dividing cambium; they focused particularly on how cambial stem cells arise. The authors conducted cell-lineage-tracing experiments, which revealed that only cells adjacent to the xylem can generate cambial stem cells. They also discovered that a single individual cambial stem cell can give rise to both xylem and phloem daughter cells, which resolves a nearly 150-year-old debate over whether this occurs. By producing daughter cells of distinct fates towards the interior and exterior of the cambium, respectively, cambial stem cells differ substantially from those in root and shoot tips. In the root tip, stem cells generally produce daughter cells in one direction only. In the shoot tip, cells acquire their fate depending on their relative final position after they have left the shoot-tip region.

Smetana and colleagues report that cambial stem cells need to receive signals from neighbouring xylem cells that are acting as organizers. The division of cambial stem cells leads to the generation of xylem and phloem daughter cells towards the root interior and periphery, respectively. This means that xylem cells acting as organizers do so only transiently, before another cell replaces

them in the position adjacent to the cambial stem cell and assumes organizer function. Smetana et al. show that the cue that determines organizer function is provided by the local accumulation of auxin, which promotes the expression of HD-ZIP III transcription factors. These, in turn, maintain the organizer cells in a non-dividing state called quiescence, which is a hallmark of this type of cell.

2. (20%)

Mammals can discriminate between a vast number of volatile compounds — perhaps more than a trillion. This extraordinary capacity is encoded by a repertoire of hundreds of olfactory-receptor genes, distributed in small groups that are present on almost all chromosomes. To ensure that the response to individual odours is specific, each olfactory sensory neuron (OSN) expresses a single, randomly selected olfactory-receptor gene. Writing in *Nature*, Monahan et al. show that, in the nuclei of mouse OSNs, certain regions of multiple chromosomes assemble in a structure that controls the expression of the full repertoire of olfactory-receptor genes in the nose, while making sure that each cell expresses only one type of receptor. These exciting findings show that interchromosomal interactions can have a determinant role in regulating gene expression.

The expression of vertebrate genes is regulated by activating genomic elements called enhancers. Enhancers can be located far from the genes themselves<sup>4</sup>, but they are typically present on the same chromosome as the gene they regulate (cis interactions). These regulatory interactions are mediated by transcription factors, assisted by other proteins, and require the participating proteins and DNA elements to be closely connected in the nucleus.

Molecular techniques, such as Hi-C<sup>5</sup>, that capture the 3D folding of chromatin (DNA and associated proteins) have revealed that the interactions between genes and their enhancers occur in compact structures called topologically associating domains (TADs) that organize chromosomes into distinct cis neighbourhoods<sup>6</sup>. Hi-C analyses have also uncovered specific interactions between genes and genomic elements located much farther away from each other, in different TADs and even on different chromosomes (these are called trans interactions). These observations raised the possibility that trans

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interactions influence gene expression. However, because the frequency of trans interactions is so much lower than that of cis interactions, their functional relevance has remained debatable.

Olfactory-receptor genes were reported to form interchromosomal clusters more than a decade ago. But the role of these clusters was unclear because deletion of potential trans enhancers affected only the expression of olfactory genes on the same chromosome. Recently, researchers from the same group as Monahan et al. identified 63 potential olfactory-receptor-gene enhancers — which they named Greek islands — distributed across 16 of the 20 chromosomes of mice. In the current paper, Monahan and colleagues provide a comprehensive and functional high-resolution analysis of the 3D organization of olfactory-receptor-gene clusters and Greek islands during the differentiation of mouse OSNs.

The authors used Hi-C to analyse the structural conformation of chromosomes in mature OSNs, the immediate progenitors of OSNs and the stem cells that give rise to these neurons. They observed interactions between olfactory-receptor-gene clusters from different chromosomes in OSNs and their immediate progenitors, but these interactions were nearly absent in stem cells. The interactions involved the entire gene clusters, and probably correspond to the aggregation of olfactory-receptor genes in an area of dense chromatin (heterochromatin) that has been seen using microscopy. This type of chromatin is associated with repressed gene expression, and probably helps to prevent the expression of more than one olfactory-receptor gene in each OSN.

### 3. (20%)

Being smart is a good thing, or so smart people like to think. Indeed, the possibility that superior cognition confers an evolutionary advantage, specifically a reproductive fitness benefit, is intuitively appealing. Of the three general fitness components—survivorship/longevity, fecundity, and mating success—the best-documented association involves survivorship. Across species, comparatively large-brained mammals and birds, which are thought to have superior cognitive capacities, show greater longevity than their smaller-brained relatives. In addition, within-species comparisons of problem-solving ability, especially in foraging contexts, have shown positive correlations with fecundity. Yet, what is arguably the most famous hypothesized fitness benefit of superior cognition has seldom been studied in

接次頁

nonhumans: the sexual selection hypothesis that clever individuals are preferred as mating partners. Recent research on several species of birds does suggest that females are attracted to males that are adept at problem-solving. In most instances, however, researchers have inferred female preference for cognitive superiority from the expression of traits (e.g., plumage or song) that correlate with cognitive performance. Unfortunately, such correlative studies cannot establish that superior cognitive ability per se is the basis of an observed mate preference. On page 166 of this issue, Chen et al. report tackling this problem by directly testing female preference for male problem-solving ability, using a small Australian parrot, the budgerigar.

Chen et al.'s approach was to observe female budgerigars choose between two males in an apparatus where they could only interact with one male at a time—a design that previously revealed preferences of female budgerigars for male plumage and vocal traits. Chen et al. did not attempt to gauge natural variation in male problem-solving ability. Instead, they tested each female with a unique set of two males to establish her relative preference for them. Then, away from the female's observing eyes, they trained the male she did not prefer to open translucent containers filled with seed. The preferred males and females, meanwhile, were exposed to already-opened containers, so they could not attempt to solve the foraging task. Next, each female was allowed to observe the trained male solve the tasks repeatedly. In alternate trials, she watched the untrained male being unable to open the containers. During this period, seed containers were present in her cage, but they were taped shut. Finally, after the observation period, each female was retested with her original set of males. Remarkably, the females shifted their preference toward the previously nonpreferred, "problem-solving" males. Control trials revealed that the shift in female preference did not result from simply observing the trained males eating seed. Nor did females exhibit a preference for other females trained on the foraging task, indicating that the main finding was specific to an intersexual context. Thus, Chen et al. offer convincing evidence that female budgerigars modified their mate preference in favor of trained males after observing them perform complex foraging tasks.

Although the main result is straightforward, its interpretation is less clear-cut. Given the growing evidence of complex cognition in an array of species, it is tempting to infer that female budgerigars preferred trained males for their apparent problem-solving prowess. However, the fact that females lacked the

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opportunity to perform the foraging task themselves suggests that they may have had little basis for understanding the exercise as a problem in need of a clever solution. Instead, they might have attributed male success in opening the containers to superior physical strength. Alternatively, the extensive training paradigm may have elicited subtle behavioral differences between trained and untrained males, such that (for example) the untrained males showed less foraging effort during the observation period or less exploratory behavior during the posttraining choice trials. Unfortunately, it is difficult to rule out such alternative explanations in most studies of comparative cognition.

Despite these concerns, the approach employed by Chen et al. has considerable promise for advancing empirical research on mate choice for cognitive traits. Numerous species display the capacity to choose mates using more than one trait, and the full set of relevant traits is not known for any species. As a result, mate choice experiments that focus on one particular set of traits almost always contain additional variation in other traits, some of which may be correlated with the traits of interest. Although the experimenters may be oblivious to those potentially confounding traits, the choosing individuals may be attending to them. Chen et al.'s approach mitigates this problem by giving the choosers additional information about their potential partners after the initial choice is made and then asking whether this additional information alters their preference. Confounding variables may still exist in such designs, especially when the additional information involves complex behavior, but they are minimized. Therefore, we anticipate that this methodology will become an important tool for mate choice research in future studies.

#### 4. (20%)

Robust daily oscillations in behavior, physiology, and biochemistry are driven by endogenous timekeeping machinery called the circadian clocks. Circadian clocks in mammals were originally considered properties of the nervous system, and the anatomical locus of this clock was determined to be the suprachiasmatic nucleus (SCN) in the hypothalamus. The neurons that make up this structure are highly interconnected (coupled) and exhibit robust and coordinated rhythms of activity, and loss of rhythmicity results in loss of behavioral rhythms such as daily activity. On page 187 of this issue, Brancaccio et al. reveal that SCNs that have been rendered "clockless" through genetic perturbation in mice can be restored to rhythmicity by rescuing

the clocks in only the astrocytes, a type of glial cell. The idea that rhythmic astrocytes are sufficient to generate a functional circadian clock that can control behavioral rhythms is surprising and suggests that the SCN can produce rhythms by means of more than one mechanism.

The SCN, a paired nucleus of ~20,000 neurons, was identified through experiments that included the introduction of lesions that rendered the animals' behavior arrhythmic, track tracing of neural circuits from the retina (which provides the light input that regulates the circadian clock), and the rescue of arrhythmic animals by transplanting fetal SCNs from donor animals with different period lengths and showing that these restored rhythms had periods of the donor animals. Although these experiments demonstrated conclusively that the SCN was necessary for circadian rhythms of behavior, subsequent discoveries of the genes and proteins that make up this timekeeping mechanism revealed that the circadian clockwork was present in nearly every cell of the body and could drive cell-autonomous rhythms independently of the SCN. Despite this, the SCN is considered the master clock that receives synchronizing light information from the environment and coordinates the rhythms of the many cellular clocks throughout the body through humoral and neuronal signals. Furthermore, the SCN has been shown to have special properties, resulting from its highly coupled neuronal network, which makes it robust and resistant to damping and to some genetic perturbations.

The core circadian clockwork consists of a transcription-translation negative feedback loop in which the heterodimeric transcription factor composed of CLOCK and BMAL1 drives expression of the repressors, including Period genes (Per1, Per2, and Per3) and the Cryptochrome genes (Cry1 and Cry2). Cells or animals with deficits in the various components of this system have compromised clocks with altered period lengths or are arrhythmic. Within the SCN, Per and Cry genes are expressed rhythmically, with a spatiotemporal wave of expression that starts from the dorsomedial edge and proceeds ventrally across the nucleus in a highly coordinated manner each day. This coupling is important for the high-amplitude robust rhythms generated by this structure, which synchronizes clocks throughout the body.

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Dissecting the roles of the neuronal cell types within the SCN has been a major focus of research. The generation of chimeric mice with different proportions and distributions of wild-type and Clock mutant cells within the SCN demonstrated that not all SCN neurons need to have an intrinsic clock in order for the ensemble to operate correctly. Other studies have used cell-type overexpression of mutant CLOCK proteins or cell-type-specific ablation of circadian clock genes to examine the roles of different cell types in driving rhythmicity. Brancaccio et al. used an opposite approach on the basis of a previous discovery that the circadian clock in mice with arrhythmic SCN in which Cry1 and Cry2 are ablated can be rescued by rhythmically expressing either Cry1 or Cry2. They used this to test the roles of astrocytes and neurons within the SCN for their ability to generate a competent SCN clock in arrhythmic mice. As expected, they found that introduction of Cry1 into either cell type in slice cultures was sufficient to rescue rhythms in the cells in which Cry1 was expressed. However, the free-running periods of the restored rhythms were different for the different cell types, with the astrocyte clock running faster than the neuron clock, demonstrating that both astrocytes and neurons are time-keepers, or pacemakers, within the SCN, but with different intrinsic properties.

Even more surprising, rescue of the astrocyte clock caused robust rhythms in gene expression in the clockless neurons. In addition, the spatiotemporal wave across the SCN was restored, suggesting that network properties within the SCN pacemaker were rescued. Furthermore, rescue of the astrocyte clock in otherwise arrhythmic mice rescued the behavioral activity rhythms, such as periodic wheel-running, demonstrating that functional circadian clocks in the astrocytes are sufficient to generate a rhythmic animal. Moreover, the free-running periods matched that of the endogenous astrocyte clock.

Brancaccio et al. determined that astrocytes with restored rhythms periodically released glutamate [a major glial neurotransmitter in the SCN] and that this glutamate was required to restore the rhythms to the SCN neurons by somehow activating the existing SCN circuit. What is not clear from these studies is whether the neuronal rhythms depend on some component(s) of the circadian clock that remain in the absence of the two Cry genes or whether the periodic glutamate directly drives the rhythms. It has been shown that SCNs of mice in which Cry1 and Cry2 are ablated have some residual rhythmicity that quickly dissipates, suggesting that some pacemaker function is still present. Additionally, loss of the Bmal1 gene in subsets of SCN neurons result in long

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periods and unstable rhythms, likely through loss of interneuronal coupling, suggesting that at least some components of the circadian clock are needed in neurons to enable normal behavior. Additional experiments using neurons that lack other components of the circadian clock will be necessary to answer these questions.

Although sufficient, astrocytes are not necessary for rhythmic behavior because neuron-only reintroduction of circadian clock genes also rescues circadian rhythms in mice, and astrocyte-specific perturbation of the circadian clock does not ablate rhythms, although it does alter the period length, suggesting that the normal clock requires interactions between these two cell types. The study of Brancaccio et al. supports the idea that the SCN has redundant and robust mechanisms for maintaining circadian rhythms, complementing earlier findings that this master timekeeper is distinctly resilient to perturbation. Clearly, the importance of maintaining rhythmicity has resulted in the evolutionary selection of many solutions for maintaining circadian rhythms.

5. (20%)

Conservation areas around the world aim to help conserve animal biodiversity, but it is often difficult to measure conservation success without detailed on-the-ground surveys. High-resolution satellite imagery can be used to verify whether or not deforestation has occurred in areas dedicated for conservation. Such remote sensing analyses can reveal forest loss and, in some cases, severe forest degradation, such as through fragmentation and intensive selective logging, especially if it includes the construction of roads or camps. However, conservation benefit is determined not only by forest loss but also by the level of degradation in those forests left standing.

Bioacoustics—specifically the recording and analysis of entire soundscapes—is an emerging tool with great promise for effectively monitoring animal biodiversity in tropical forests under various conservation schemes.

Even forests that appear intact in satellite imagery can have low biodiversity conservation value because of effects such as canopy simplification, understory fires, invasion by exotic species, or overhunting. These forms of degradation are difficult to monitor remotely with satellite imagery, resulting in a common but faulty assumption that conserving forest cover is necessarily

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equivalent to conserving biodiversity. Continuing advances in spectral imagery and lidar (light detection and ranging) reveal progressively finer levels of forest change, but they still remain a proxy for animal biodiversity rather than a direct measure of it.

Repeated on-the-ground surveys can provide the required information to assess animal biodiversity. However, such surveys are expensive, cover limited ground, and may be affected by the biases of individual experts. One possible alternative is the use of bioacoustics, which can detect animals by their vocalizations. Depending on vegetation structure and the vocalizing species, acoustic recorders can detect animal calls and song from several hundred meters away. Autonomous sound-recording devices are now available from several companies as small units that are inconspicuous to humans. They can be programmed to record either continuously, if there is sufficient solar power or cellular network signal for direct transmission of data to cloud storage, or at given intervals, if battery power and data storage are limiting factors. Several multiyear recordings have now been completed.

Selected times of the day can convey a disproportionately large amount of information about the resident biodiversity; for example, mornings and evenings have been found to be particularly important for detecting differences between forests that are used in different ways by humans. With further developments in energy and data storage and transmission, continuous recording is likely to become the norm.

Relative to on-the-ground surveys, bioacoustics is inexpensive, making it more feasible to repeat measurements over time. Also, the results are not influenced by individual researchers' biases or simply by the presence of observers in the field. The method offers the possibility to monitor multiple taxonomic groups at the same time (all vocalizing birds, mammals, insects, and amphibians), as opposed to, for example, camera traps. Finally, the data can be reanalyzed in the future with improved algorithms or to search for specific acoustic features. Analysis of human-made sounds can help to clarify how sounds from machinery (such as tractors, bulldozers, and chainsaws) affect habitat quality and to track illegal human activities, such as gunshots from poachers or chainsaws in illegal logging.

Acoustic data from soundscapes can be analyzed in many ways. Various

接次頁

indices can be calculated that characterize the soundscape for each time and frequency unit. Alternatively, individual species can be identified by experts, algorithms, or deep learning.

Soundscape analysis using indices appears most suitable to monitor the general state and recovery of forests, because it does not require site-specific species lists. Random forest models based on multiple acoustic indices can predict species richness with very high accuracy. However, further studies linking on-the-ground biodiversity surveys to soundscape indices are needed from a wide variety of forest types and human disturbances to determine whether such indices can be generalized. In areas where hunting is important, the recordings could also be used to determine the presence or absence of the hunted species (typically large mammals and birds) using individual species recognition algorithms.

Bioacoustics has particular potential in the context of industry sustainability certification and zero-deforestation commitments, both of which have become popular, widely publicized conservation strategies. Companies involved in such industries as palm oil, beef, soy, and pulp and paper production commit to not cause any deforestation through their industrial development. Typically, this means that any new plantation, ranch, or farm can only be developed in an area that is already deforested or heavily degraded. In some countries, such as Brazil, companies are legally obliged to protect parts of their concessions from deforestation. However, precise definitions of zero deforestation are often missing. The conservation benefit of such industry-protected forests should be determined not just by how much forest loss has been avoided, but also by the level of biological integrity of those forests left standing. Bioacoustics has the potential to provide this information.

Advances in bioacoustics, as well as the robustness and affordability of sound-recording devices, make it possible for companies or independent consultants to deploy sound recorders in areas of forest maintained by a company under legal requirements, certification, or a zero-deforestation commitment. If the soundscape of a forest spared from conversion were becoming more impoverished and altered beyond the natural variation of the soundscape baseline, on-the-ground survey would be warranted. Slow, gradual changes in soundscape composition due to climate change might be beyond the direct control of the companies, but abrupt and quick change in

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soundscapes is more likely to be attributable to management. In these cases, other measures (such as prevention of hunting, reforesting edges or the degraded areas of the conserved zone with native species, or curbing fires) would be called for by auditors, who are typically involved in independent verification of a company's commitments.

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