

3. Wagner, J.K., Setayeshgar, S., Sharon, L.A., Reilly, J.P., and Brun, Y.V. (2006). A nutrient uptake role for bacterial cell envelope extensions. *Proc. Natl. Acad. Sci. USA* *103*, 11772–11777.
4. Piatigorsky, J., and Wistow, G. (1991). The recruitment of crystallins: new functions precede gene duplication. *Science* *252*, 1078–1079.
5. True, J.R., and Carroll, S.B. (2002). Gene co-option in physiological and morphological evolution. *Annu. Rev. Cell Dev. Biol.* *18*, 53–80.
6. Blount, Z.D., Barrick, J.E., Davidson, C.J., and Lenski, R.E. (2012). Genomic analysis of a key innovation in an experimental *Escherichia coli* population. *Nature* *489*, 513–518.

Department of Molecular Biology, Princeton University, Lewis Thomas Laboratory, Room 355, Princeton, NJ 08544, USA.  
\*E-mail: [zgitai@princeton.edu](mailto:zgitai@princeton.edu)

<http://dx.doi.org/10.1016/j.cub.2014.04.022>

## Ecology: Honey Bee Foraging in Human-Modified Landscapes

Comprehensive information on the spatial resource use of honey bees is rare, but highly relevant to assess the consequences of habitat loss and fragmentation, agricultural intensification or extensification on colony fitness, pesticide exposure risks and pollination functions.

Stephan Härtel\*  
and Ingolf Steffan-Dewenter

European landscapes have been highly modified by human impact with habitat fragmentation, habitat conversion and agricultural land use intensification as major processes [1]. As a result most landscapes are characterised by a mix of different habitat types with varying proportions of natural, semi-natural, agricultural and urban areas. The transformation of landscapes and the increase of human land use have severe negative impacts on biodiversity in landscapes dominated by intensive agriculture [2,3] and threaten important ecosystem functions such as pest control and pollination of crops [4–6]. European agri-environmental schemes such as organic farming have been implemented to counteract biodiversity loss and maintain ecosystem services, but their effectiveness depends on more elaborated conservation measures, selection of organism groups and landscape structure [7,8]. An important aspect here is the provision of additional resources such as pollen and nectar for pollinators in a landscape and the way organisms are able to locate and use it for reproduction [9,10].

In the case of the honey bee with an estimated foraging range of 100 km<sup>2</sup> [11], it is simply impossible to gain a detailed spatial picture of floral food resources and their use by bee foragers by direct observations. In particular, it is difficult to link flower-visiting bees to a certain colony and the location of nesting sites in the

countryside. However, honey bees offer the opportunity to ‘eavesdrop’ on the internal communication system to understand food recruitment and spatial resource use in more detail. A successful forager communicates rewarding food locations via the well-known waggle dance to her nest mates. This behaviour can be regarded as one of the most fascinating phenomena in the insect kingdom.

Pioneering experiments conducted by von Frisch (1965) [12] and Seeley (1995) [11] opened the door to a unique perspective from the bee colony to the surrounding landscape and its resources. In the last decades, the dance language has been intensively studied as a fascinating mode of communication to understand basic mechanisms of in-hive organisation and behavioural physiology [11]. However, surprisingly few studies use the dance language to address ecological questions, and in particular landscape-wide analyses of foraging patterns are almost absent (but see [13–15]). As a consequence, foraging and resource use of honey bees on a broader landscape scale is simply under-investigated. Several studies used the capacity of honey bees to monitor environmental pollution [16], but the idea to take advantage of waggle dance information to evaluate agri-environmental schemes on a landscape scale has not been developed so far. In this issue of *Current Biology*, Margaret Couvillon and co-workers [17] applied this approach in a year-round analysis of the spatial resource use of three honey

bee colonies in a mixed agricultural landscape in England.

Over two years they decoded more than 5,600 bee dances and plotted the location of used flower resources on geographical maps; they show how different habitat types with or without different agri-environmental schemes are preferred or avoided in a foraging area of close to 100 km<sup>2</sup>. They find a significant preference of foraging honey bees for nature conservation areas under high level stewardship and, more surprisingly, low preference values for organically managed farm land. These results are novel due to two innovative methodological achievements. Firstly, the authors corrected for distance to take into account the higher energy expenditure of more distant floral resources when they calculated habitat preferences. Secondly, Couvillon *et al.* included naturally occurring variations within the dance communication in their models. These tools will significantly improve future research on spatial and temporal patterns of resource use by honey bees. While we applaud the achievements made in this study, we are also excited about the future perspectives and so far unexplored aspects of honey bee foraging in agricultural landscapes. The revealed preference of foraging honey bees for nature reserves not only underlines the resource richness of these habitats and their value for honey bees, it also indicates that the spatial overlap in resource use with threatened wild bee species might be higher than previously assumed [18]. Using honey bee colonies as bioindicators to identify the location of high-resource patches in a landscape, as suggest by Couvillon *et al.* [17], might thus also help to quantify the competitive pressure by honey bees on other flower-visiting insects in conservation areas [19].

Human-dominated landscapes are characterised by high spatial and temporal dynamics of cropping

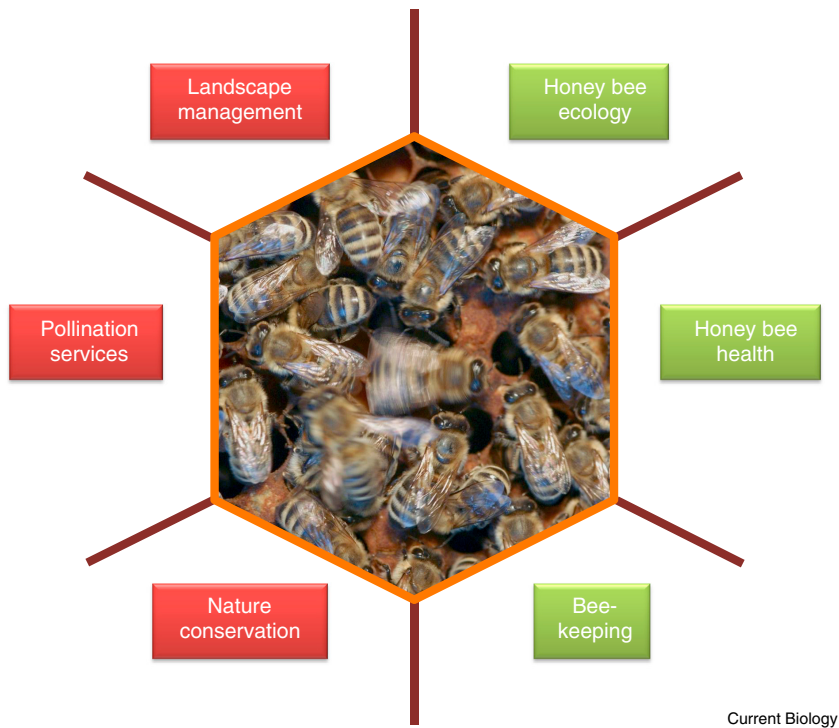


Figure 1. Exploiting the waggle dance.

The spatial information encoded in the unique dance communication of honey bees could deliver valuable data for general (red) and honey bee-specific (green) research fields and topics. (Photo: M. Kleinhenz, HOBOS-Team.)

patterns and management activities. Consequently, floral resources from mass-flowering crops, set-aside fields and other habitats are often available only for short time periods [10]. Habitat types which provide only temporary resources might be undervalued by the Couvillon *et al.* approach, which levels preferences over a two-year period and therefore might have missed the value of resource pulses provided, for example, by oil seed rape or sunflowers [20]. Thus, the detailed analyses of bee dances at higher temporal resolution can provide little known insights into the dynamics of resource use. Another important topic is the spatial variation of landscape composition and configuration, from complex and extensive to homogeneous and intensively managed landscapes, and its consequences for foraging locations and distances [15]. One important applied aspect in this context is the question to what extent do foraging honey bees provide crop pollination services in intensively managed landscapes with low pollinator diversity. The distribution of foraging honey bees in agricultural landscapes could reveal spatial gaps in

the provision of crop pollination services and could direct landscape management of pollination services.

The decoded dance language also has the potential to fill in gaps in our knowledge beyond ecological questions. Further, both honey bee-specific as well as related fields could benefit from the analysis of spatial resource utilization of honey bee colonies (Figure 1). Implementing such information could eventually be a key element in the understanding of factors related to the globally observed mismatch between pollinator requirements of insect pollinated crops and regional honey bee populations, which are declining [5]. The spatial information of where honey bees find diverse pollen resources in the flight range would help to identify and promote structural landscape characteristics with positive impacts on honey bee colonies and other insect pollinators. Landscape-wide analysis of crop pollen and nectar recruitments could help to estimate spatial pesticide exposure risks in intensive agricultural settings. Future studies could also consider how foraging landscapes are related to colony development, honey

yields and overwintering mortality to optimise the economic and ecological revenues of beekeeping. Linking such information to the spatial and temporal dynamics of mass-flowering crops, agri-environmental schemes, pesticide applications, and genetically modified crops would help to assess important questions in the context of environmental risk assessment, management of pollination services and biodiversity conservation in human-dominated landscapes.

#### References

1. Tschamtkke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecol. Lett.* 8, 857–874.
2. Kleijn, D., Kohler, F., Baldi, A., Batáry, P., Concepción, E.D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., *et al.* (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc. R. Soc. London B. Biol. Sci.* 276, 903–909.
3. Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., and Sait, S.M. (2013). Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biol. Rev.* 88, 1002–1021.
4. Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., *et al.* (2011). The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecol. Appl.* 21, 2187–2196.
5. Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., *et al.* (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.
6. Martin, E.A., Reineking, B., Seo, B., and Steffan-Dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proc. Natl. Acad. Sci. USA* 110, 5534–5539.
7. Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., *et al.* (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* 9, 243–254.
8. Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., and Kleijn, D. (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecol. Lett.* 16, 912–920.
9. Andersson, G., Birkhofer, K., Rundlöf, M., and Smith, H. (2013). Landscape heterogeneity and farming practice alter the species composition and taxonomic breadth of pollinator communities. *Basic Appl. Ecol.* 14, 540–546.
10. Holzschuh, A., Dormann, C.F., Tschamtkke, T., and Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia* 172, 477–484.
11. Seeley, T.D. (1995). *The Wisdom of the Hive* (Harvard University Press).
12. von Frisch, K. (1965). *Tanzsprache und Orientierung der Bienen* (Berlin, Heidelberg, New York: Springer).
13. Waddington, K.D., Visscher, P.K., Herbert, T.J., and Richter, M.R. (1994). Comparisons of forager distributions from matched honey-bee colonies in suburban environments. *Behav. Ecol. Sociobiol.* 35, 423–429.

14. Beekman, M., and Ratnieks, F.L.W. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Funct. Ecol.* *14*, 490–496.
15. Steffan-Dewenter, I., and Kuhn, A. (2003). Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. London B. Biol. Sci.* *270*, 569–575.
16. Kevan, P.G. (1999). Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agric. Ecosyst. Environ.* *74*, 373–393.
17. Couvillon, M.J., Schürch, R., and Ratnieks, F.L.W. (2014). Dancing bees communicate a foraging preference for rural lands in high level agri-environment schemes. *Curr. Biol.* *24*, 1212–1215.
18. Steffan-Dewenter, I., and Tschamtkke, T. (2000). Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* *122*, 288–296.
19. Hudewenz, A., and Klein, A.-M. (2013). Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. *J. Insect Conserv.* *17*, 1275–1283.
20. Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., and Holzschuh, A. (2014). Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecol.* *29*, 425–435.

Department of Animal Ecology and Tropical Biology, Biocenter, Am Hubland, 97074 Würzburg, Germany.  
\*E-mail: [stephan.haertel@uni-wuerzburg.de](mailto:stephan.haertel@uni-wuerzburg.de)

<http://dx.doi.org/10.1016/j.cub.2014.04.052>

## Cytoskeleton: Cirque du Septins

**Septins and F-actin are familiar cohabitants of the cleavage furrow yet how they might be functionally connected has been ambiguous. New work shows that septins can promote the assembly of curved bundles of F-actin, providing an unexpected molecular function for septins in cytokinesis.**

Amy S. Gladfelter

Circles are found throughout life from fairy rings to ring canals. Mark Twain made it sound so easy to build a circle when he quipped that a circle was just “a round straight line with a hole in the middle”. However, the problems of how cells build rings to be a precise size, to dynamically change size and do work have engaged cell biologists for decades. The cytokinetic ring, responsible for the mechanics of separating one cell into two, has become one of the most intensively studied cellular circles.

Septin proteins are a central component of the cytokinetic ring in many animals and fungi. In some contexts, pure septins can self-assemble into ~500 nm circles *in vitro* or seemingly spontaneously on plasma membranes *in vivo* [1,2]. Septin assemblies are built out of heteromeric complexes of septins that form rods of 32–40 nm in length that can also polymerize into longer filaments [3–5]. Despite their propensity to form rings and their localization to the cleavage furrow, what septins actually contribute to cytokinesis mechanistically has been remarkably difficult to tease apart. Septins have been invoked as scaffolds, membrane organizers and diffusional barriers at the cleavage furrow but there is still limited molecular or biophysical data supporting these proposed roles. Recent work from Mavrikis *et al.* [6] now provides detailed evidence that

septins can bundle actin filaments and likely does this to organize actomyosin rings, the contractile unit in the cytokinetic apparatus.

Mavrikis *et al.* discovered this role for septins in forming curved bundles of F-actin by studying embryonic cleavage during cellularization of *Drosophila*. Cellularization is a specialized cytokinesis involving the compartmentalization of thousands of nuclei, previously cohabitating one cytoplasm, into individual cells. Ingressing membranes form the walls between nuclei, and the tip of this membrane, the furrow canal, is evocative of the cytokinetic ring both in terms of the molecular components and function. In embryos lacking the septin called Pnut, the actomyosin ring assembles with different kinetics and with less Myo-II protein present, the actin motor that can help drive constriction. This aberrant assembly leads to both slowed membrane ingression and actomyosin ring constriction rates. The source of these problems is not likely a defective septin-dependent diffusion barrier at the furrow canal, an attractive hypothesis due to the geometry of the structure and models of septins acting as gaskets to trap the cytokinetic machinery.

The root of the constriction delays rather seems to be highly disorganized actin. Instead of forming compact circles, in septin mutants the F-actin is in straight bundles that create polygonal-shaped compartments. After discounting that the phenotypes were

due to reduction in Myo-II or mislocalized Anillin, another key player in the contractile ring, the authors closely examined the ultrastructure of F-actin in furrow canals for the first time. Cortical actin was more diffuse and disorganized in septin mutant cells when examined using transmission electron microscopy (TEM). Given the difficulty in deciphering individual actin filaments *in vivo* by TEM, the authors implemented polarized fluorescence microscopy to better determine the orientation of actin filaments in septin mutants. Polarization analysis revealed that actin bundles are highly ordered, comparable to actin in a stress fiber, and oriented parallel to the furrow canal membrane in wild-type cells. In septin mutants, however, the degree of order was diminished and the orientation of filaments was highly variable.

All combined, the data point to actin disorganization as the source of the problems, but what is the cause of this defect? No direct association between septins and actin had ever been shown, until now. Mavrikis *et al.* were able to show direct binding of septins to F-actin, and the capacity of septins to bind and bundle F-actin is comparable to well established actin binding proteins. This is already very exciting but the effect was spectacular when the septin-actin mixtures were viewed under TIRF (Total Internal Reflectance) microscopy and dramatic arcs, swirls and, indeed, circles of actin could be seen. Notably, both fly and human septins could create highly curved bundles of actin *in vitro*. Further experiments suggest, albeit with a few possible caveats, that septins likely promote this curvature in their small, rod state rather than in a filamentous state. If true, promoting curved actin bundles is the first function ascribed to septins in their subunit rather than filamentous form.