by the counteracting phosphatases (Figure 1B). While phosphatase docking is much less studied, recent work suggests it may be prevalent and, intriguingly, overlap with kinase docking. The protein phosphatase 1 docking site on the retinoblastoma protein overlaps with the known docking site for S phase cyclin–Cdk [12]. A new study examining Ca^{2+}/calmodulin-regulated phosphatase (CN) showed that its docking specificity overlaps with that of the pheromone-activated MAPK Fus3 [13]. This presents two examples where competing kinase–phosphatase pairs recognize the same docking site, which might enhance switch-like transitions of the phospho-state of individual targets. In addition, we are immediately provided with a mechanism through which competition between kinase–phosphatase pairs can be conserved. Goldman *et al.* [13] compared kinase and CN targets in mammals and yeast to find that while nearly no specific substrates were conserved, the same kinases opposed CN on both sets of substrates. To evolve co-regulation of a substrate by a specific kinase–phosphatase pair with overlapping docking specificity, mutation only needs to generate a single docking site, rather than two. Thus, overlapping docking specificity may explain why the same network functions are regulated by the same kinases and phosphatases across diverse eukaryotes.

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Coevolution: Puff Pollination in Tropical Flowers

A new study shows that birds plucking anthers of the Melastome, *Axinaea*, demonstrate a novel bird pollination mechanism. Each stamen of *Axinaea* offers a nutrient-rich, berry-like food body that, when bitten, releases a puff of pollen allowing transfer to stigmas by wind or the pollen-dusted bird.

Joan Edwards

Flowers and their pollinators offer a palette of diversity to study coevolution and provide data for unraveling Darwin’s “abominable mystery”, the sudden appearance and extraordinarily rapid diversification of the angiosperms [1]. Yet with over 350,000 species of flowering plants [2], we are still discovering new methods of pollination. For New World bird pollination syndromes we typically think of tubular red flowers, copious amounts of dilute nectar, and the whirr of hummingbirds hovering as they collect nectar through specially engineered tongues [3,4]. Not so for the novel bird pollination system reported for the neotropical Melastomataceae, *Axinaea*, by Dellinger *et al.* in this issue of Current Biology [5], adding a new twist to our thinking about how birds can effect pollination and how pollination syndromes can develop.

For *Axinaea* flowers, the bird pollinators are not hummingbirds, but a diverse group of tropical fruit-eating tanagers. Flowers vary in color from white to pale lavender to red and offer no nectar reward, but instead provide berry-like food bodies rich in citric acid, fructose and glucose (Figure 1A). In return for the food bodies, the birds power a uniquely designed bellows pollination system, where the bite of the bird’s beak releases a puff of pollen that is either carried by wind or by pollen-dusted birds depositing pollen on the exerted stigmas of the next flowers they visit.

The authors document this system with detailed analyses of stamen morphology. Using X-ray computed tomography, SEM and thin sectioning, they present stunning 3-D images and longitudinal cross-sections illustrating the anatomy of the anthers. Each of the ten anthers in the flower is modified to be a miniature turkey baster where the ‘bulb’ is the nutritious food body made up of large air-filled cells that connects to the ‘shaft’ made of pollen-filled anther sacs with a pore-sized opening at the end. The whole operation points downward to the center of the flower, so that when the bird plucks the food body, it forces air from the food body into the anther sacs and releases a pollen puff that is directed towards the top of the flower and the bird’s head and beak (Figure 1B).

Figure 1. Co-evolution of a flower and its pollinator.

(A) Flower of *Axinaea costaricensis,* showing five mature anthers with large white food body appendages. The tubular magenta anther sacs extend from the base of each food body. (B) A schematic showing how birds pluck and squeeze the food body causing a puff of pollen to exit the anthers from the apical pore. The pollen can then be transferred to stigmas by wind or by birds when visiting other flowers. (C) *Chlorospingus pileatus* (sooty-capped bush tanager) holding a food body and anther sac from *A. costaricensis*. The food bodies primarily provide sugars and vitamin C. Credits: (A) Photo cropped from image by Juan Franscisco Morales (http://melas-centroamerica.com/axinaea-costaricensis/); (B) drawing by Ann Kremers; (C) photo by Florian Etl.

The biomechanics of this puff pollination system depend completely on the power of the beak. Spores, including pollen, are perfect for dispersal in puffs, but the dilemma plants and fungi face is how to power the puffs. The small size of spores means they have a low terminal velocity and thus require substantial force to move any distance. Puffball fungi harness the energy of falling raindrops [6]. Sphagnum moss builds pressure in capsules that eventually blow their tops propelling spores in vortex rings [7]. In angiosperms, both bunchberry dogwood [8] and white mulberry [9] use stored mechanical energy in their catapult-like stamens to power pollen puffs. Here, the flowers co-opt the force of the bird's beak to power the puff.

The fruit-like traits of the food bodies may have predisposed fruit-eating birds to be attracted to the stamens of *Axinaea* flowers, thus initiating the bellows pollination system. The food bodies themselves are modified anther connective tissue. They are clearly berry-like with high food value and bright colors that markedly contrast with bowl shaped flower corollas (Figure 1). Although each food body is tiny, on a per weight basis, the measure of caloric gain from the food bodies averages 3.61 kcal/g, just slightly less than the calories in sugar (3.81 kcal/g) and slightly more than the calories in raisins (3 kcal/g) [10]. This is not surprising since the metabolomic analyses (gas chromatography and mass spectrometry) show the food bodies are high in the hexoses, sucrose and glucose, and also high in vitamin C.

The stamen structure in the Melastomataceae may have predisposed them to develop into the miniature bellows we see in *Axinaea*. Most members of the Melastomataceae are buzz pollinated [11] where the pollen is released from anthers in response to the vibrational buzz of bees. Typical buzz-pollinated flowers have poricidal anthers and dry, smooth-walled pollen for easy release when buzzed [12]. These general buzz-pollination features are also effective for the puffs produced by the bellows. But in addition, Melastome anthers often have stamen appendages, which are an extension of the connective tissue. In other species these may serve to enhance floral displays or to facilitate buzz pollination, but in *Axinaea* they have been modified to be sugary food bodies with air-filled cells.

The phylogenetic diversity of the bird visitors and the differences in visitors among sites suggests that the association between *Axinaea* and birds may have evolved independently in different locations. *In situ* observations including over 200 hours of video show that for the three species of *Axinaea* observed, birds are the only pollinators. All six bird species observed visiting *Axinaea* are known fruit and insect eaters [13], predisposing them to feed on the berry-like anthers. All are nine-primaried oscines, a large diverse group that radiated recently in the neotropics [14,15]. However, within this large clade the birds observed on *Axinaea* surprisingly are not all closely related. Three species visiting *A. confusa* are closely related montane tanagers, but the orange-bellied Euphonia (*Euphonia xanthogaster*) observed on *A. confusa*, the bush tanager (*Chlorospingus pileatus*) (Figure 1C) observed on *A. costaricensis*, and the masked flower piercer (*Diglossa cyanea*) observed on *A. sclerophylla* are all in separate distantly related groups [14,15].

The ecological flexibility of the system where different birds can effect pollination may contribute to the persistence of some *Axinaea* species. *Axinaea* is a neotropical genus, with 39 species of small trees and shrubs that are primarily restricted to the Andes between 1200 and 3800 m with *A. costaricensis* occurring further north in Costa Rica and Panama [16,17]. Within this genus some species, including *A. sclerophylla* in this study, are considered rare due to small population sizes or distributions limited to one locale in unprotected areas [17,18]. The observation of different birds at different sites suggests a generalist system where the flowers in each locality can draw on the local birds for pollination services.

Biologists have long been fascinated by pollination syndromes, easily characterizing flowers by floral features that are adaptive for attracting specific pollinators, thus allowing targeted gene flow among the 350,000 plus angiosperms, 94% of which use biotic vectors for pollination [19]. Indeed, the directed gene flow itself is an explanation for Darwin's abominable mystery. But increasingly as we explore plant–pollinator systems with a more careful eye, the simplicity of pollination syndromes seems much less applicable. The *Axinaea*–bird system is a case in point as it deviates from the hummingbird pollination system, provides insight into how syndromes or clusters of traits can evolve in pollination systems, and presents a case for ecological flexibility, which may contribute to the persistence of angiosperm species in complex communities.

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Centrosome Duplication: Suspending a License by Phosphorylating a Template

The phosphorylation status of Sfi1, a structural component of the yeast centrosome, governs the centrosome duplication cycle, raising the possibility that licensing of centrosome duplication occurs by modulating Sfi1, which potentially acts as a template for a new centrosome.

Kayoko Tanaka

The centrosome is a fascinating single copy organelle present in almost all higher eukaryotic cells. It acts as the major microtubule organizing centre (MTOC) as well as a platform for various cell proliferation and differentiation regulators [1,2]. Apart from the centrosome's divergent fundamental roles, its mode of duplication has intrigued us for decades — it occurs strictly once per cell cycle in a semi-conservative manner. Failure to keep precise control over centrosome number is often associated with malignant tumor cells [3,4]. In a recent issue of *Current Biology*, Schiebel and coworkers reveal that cell-cycle regulatory kinases and a phosphatase tightly regulate the centrosome duplication cycle by targeting Sfi1, a structural component of the yeast centrosome [5].

The direct link between the cell cycle and the centrosome cycle has spurred studies examining whether key cell cycle regulators, including cyclin-dependent kinases (CDKs), Polo-like kinases and separase, also play roles in the centrosome cycle [6–9]. Together, these findings have revealed that centrosome duplication is 'licensed' once per cell cycle. The concept of licensing was originally introduced through studies of DNA replication where the key licensing step is the loading of pre-replicative complexes prior to the unwinding of double-strand DNA [10]. In the context of centrosomes, licensing involves the process of centriole 'disengagement', an event where two orthogonally placed centrioles becomes detached in late mitosis [11]. A protease called separase, which becomes active in anaphase, is required for disengagement, and the loosened centrioles are expected to expose the site of duplication for the next round of duplication [9].

More direct involvement of structural component(s) of the centrosome in the licensing process was proposed by Kilmartin and colleagues based on elegant studies of spindle pole bodies (SPBs), the centrosome equivalent in budding