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metry and conventional radiocarbon dating of bulk peat samples from the lowest visually apparent peat horizon in each core. Substantially older radiocarbon ages from organic-rich gytjja (mineral substrate) were excluded from new data presented in this paper. Samples were processed by Beta Analytic, Incorporated (Miami, FL) and calibrated with the use of CALIB 4.3 (35) and the Intcal98 data set.

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23. Our estimates of WSL peatland extent (592,440 km²) and total carbon pool (70.2 Pg C) have their basis in a comprehensive GIS-based inventory of all peatlands throughout the region. Data sources assimilated are (i) an archive of printed data reports based on ~40 years of field surveys by Geoltorfrazvedka, Moscow, beginning in the 1950s, with updates by the Russian Ministry of Natural Resources in the 1990s. These reports contain detailed maps with associated field and laboratory measurements of peatland depth, area, bulk density, and ash content for 9691 peatlands throughout the WSL, for a total of 29,350 measurements digitized. (ii) Our own field data collected from 1999, 2000, and 2001, including peat physical properties from 87 cores, 78 additional measurements of peatland depth, and 16 ground-penetrating radar transects. (iii) A Russian typological wetland map extending coverage beyond that of the Geoltorfrazvedka reports. (iv) Visible/near-infrared MSU-SK satellite images from the Russian RESURS-01 satellite. (v) 62 additional depth measurements gleaned from the published literature. Because of the flat terrain, WSL peatlands are broadly expansive with little depth variation. Ordinary kriging of all available depth data therefore allowed reasonable interpolation of missing values for 3904 of 9691 peatlands inventoried. All data were digitized and incorporated into a ARC 8.2 GIS database and together cover the entire WSL. Total carbon pool (CP) was computed as

$$CP = \left(\sum_{i=1}^{n} A_i \cdot D_i \cdot r_i \cdot [(100-a_i)/100] \cdot c \right)$$

where n is the number of digitized peat polygons (9691) and A_i, D_i, r_i, a_i, and c represent peatland area, mean depth, depth-averaged bulk density, depth-averaged ash content, and organic carbon fraction (52%), respectively.
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25. The lower (oldest) sections of our cores are dominated by fen species Scorpidium sp., Calliergon sp., and Drepanocladus sp., with later succession to bog species Sphagnum fuscum and S. angustifolium that dominate the WSL ecology today. Modern transfer function–derived methane fluxes for these fen species average about six times higher than for these bog species (26), suggesting substantially higher WSL methane emission in the early Holocene.
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30. Desiccation of WSL peat carbon stocks would elevate atmospheric CO₂ concentrations through peat oxidation but reduce CH₄ emissions through associated drying. Because of high temporal and spatial variability in contemporary rates of CH₄ emission, it is difficult to estimate the potential net radiative balance of these opposing effects. However, even in an

extreme (and unlikely) scenario, assuming (i) complete oxidation of all WSL peat carbon stocks in the next 500 years, (ii) a complete shutdown of all WSL methane emission during the same 500 years, (iii) a 2.5-fold greater infrared absorptivity of CH_4 relative to CO_2 [because of the shorter lifetime of CH_4 in the atmosphere, the greenhouse radiative forcing of CH_4 is only ~2.5 times that of CO_2 when integrated over a 500-year time scale (29)], and (iv) high WSL methane flux at present (~14 Tg CH_4 year^{-1}, calculated as 600,000 km² × 120 day year^{-1} × 195.3 mg CH_4 m^{-2} day^{-1}), the resulting release of ~11.7 × 10^{12} mol CO_2 year¹ (from oxidation) would be effectively reduced by 2.2 × 10^{12} mol CO_2 year^{-1} (the radiative equivalent of the loss of 8.7 × 10^{11} mol CH_4 year^{-1} emission), or only ~18.8%.

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34. Fine debris fraction (percentage of peat fragments ≤150 μm) was measured with the use of the following variation of the ASTM (American Society for Testing Materials) Fiber Weight Method (33). Two-mL peat subsamples were taken every 10 cm throughout all cores, soaked for 12 hours in a dispersing agent (5% sodium hexametaphosphate) and washed through a 150-μm sieve. Coarse debris content (f_{150}) was computed as the ratio of oven-dried mass (100°C) of this fraction relative to that of a complete sample. Percent fine fraction was computed as (1 – f_{150}). To identify the possible influence of

species assemblage on f_{150}, we visually assessed macrofossil taxonomies (as percentage of total) with the use of light microscopy. Regression of (1 – f_{150}) with core depth and macrofossil abundances within five functional or taxonomic groups (Sphagnum, brown moss, sedge, herbacious, and woody plants) shows that less than 12% of the linear variance in (1 – f_{150}) is associated with these factors (r^2 = 0.114; P < 0.0001), allowing the assumption of external influence (i.e., changing acrotelm temperatures and water table position) on f_{150}.

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Community Assembly Through Adaptive Radiation in Hawaiian Spiders

Rosemary Gillespie

Communities arising through adaptive radiation are generally regarded as unique, with speciation and adaptation being quite different from immigration and ecological assortment. Here, I use the chronological arrangement of the Hawaiian Islands to visualize snapshots of evolutionary history and stages of community assembly. Analysis of an adaptive radiation of habitat-associated, polychromatic spiders shows that (i) species assembly is not random; (ii) within any community, similar sets of ecomorphs arise through both dispersal and evolution; and (iii) species assembly is dynamic with maximum species numbers in communities of intermediate age. The similar patterns of species accumulation through evolutionary and ecological processes suggest universal principles underlie community assembly.

Community assembly has intrigued biologists for decades (1), leading to a sophisticated understanding of the ecological parameters that dictate community membership (2). The role of evolution in shaping communities is also well appreciated (3, 4), although the steps through which communities are assembled as a result of evolutionary processes have been enigmatic. Adaptive radiations on remote islands provide opportunities to study multiple communities, each

comprising closely related organisms—a feature that has produced insights into evolutionary patterns of species composition and number (5). In particular, two patterns have emerged: (i) A predictable number of species can exist for a given area on remote islands, apparently driven by higher rates of speciation on larger islands (6); and (ii) the end-product of adaptive radiation is often a nonrandom set of species, with lineages diversified in such a way that the same set of ecomorph types occur on each island (7, 8). These findings suggest that evolution on more remote islands can act in a manner analogous to immigration on less remote islands, giving rise to similar spe-

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cies numbers and communities. What has been missing is knowledge of the historical processes that underlie these present-day patterns. Volcanic "hot spot" archipelagos provide a natural experiment for observing processes of adaptive radiation. In the Hawaiian Islands, the extreme isolation, topographical diversity, and chronological series of islands [from Kauai, formed 5 million years ago (Ma), to Hawaii, formed <1 Ma], illustrate different stages in an adaptive radiation, thus revealing the historical series of events that lead to the present.

The largest spider radiation in the Hawaiian Islands belongs to the genus *Tetragnatha* (Tetragnathidae), which includes several closely related lineages. The best known lineage is the monophyletic "spiny leg" clade of 16 species that have abandoned web-building, developed long spines along their legs, and hunt through active pursuit of prey (*9*, *10*). Species of spiny leg *Tetragnatha* spiders exhibit four distinct types (ecomorphs) of different color and size that can be mapped directly to one of four ecological roles (Fig. 1) (*11*). The "green" ecomorph is an actively moving, leaf-dwelling spider that feeds mostly on small flying insects.

The "maroon" ecomorph is mostly moss-dwelling and feeds on weakly flying insects. The "large brown" ecomorph is slow-moving, associated with tree bark, and feeds largely on Lepidoptera larvae. The "small brown" ecomorph is actively moving, inhabits twigs, and feeds on very small flying insects. I investigated first the ecological roles of different spider species, then the evolutionary origins of the ecomorphs, and finally the dynamics of community assembly, using a phylogenetic hypothesis of relationships in the context of the chronological history of the Hawaiian Islands.

Within any single community, two to four different ecomorphs co-occur (*9*, *10*). Similar sets of the different ecomorphs occur in most native habitats, regardless of volcano age, and the assemblage of species on each island is highly significantly nonrandom (Fig. 2). Not all localities have all ecomorphs, but at any given site, there is never more than one species representing a given ecomorph, and different species of the same ecomorphs have distinct parapatric distributions. The finding that similar ecomorphs never co-occur is most apparent on East Maui. Here, each of the ecomorphs is represented across most of the northeast slope, yet the species composition of the array of four ecomorphs changes markedly between locations.

Historical hypotheses were generated to determine whether ecomorphs evolved once and

spread among volcanoes and islands by dispersal, or whether ecomorphs evolved multiple times and converged on similar morphologies and ecological functions. I compiled two data sets consisting of DNA sequences (from three mitochondrial gene regions) and allozymes. Analyses of both showed that species clustered within islands, indicating multiple independent evolutionary origins of ecomorphs (Fig. 3). The most ubiquitous green ecomorph may have evolved either (i) once at the base of the clade with multiple (at least four) losses, or (ii) at least three times, once on each of the older islands, Kauai (*Tetragnatha kauaiensis*) and Oahu (*T. tantalus* and *T. polychromata*), as well as on the Maui, Molokai, and Lanai complex of islands, referred to as Maui Nui (*T. brevignatha*, *T. macracantha*, and *T. waikamoi*). Likewise, the maroon ecomorph has evolved independently on Oahu (*T. perreirai*) and Maui Nui (*T. kamakou*); both species are closely related to a green ecomorph with which they co-occur. One of the small brown ecomorphs (*T. restricta*) has also evolved independently on Maui. Yet, species formation is not always associated with change in ecological role, because some species with the same ecomorph have dispersed between islands. For example, the small brown species are mostly related to species of the same ecomorph on other islands. The large brown ecomorph is unusual in that,

Fig. 1. Examples of the four ecomorphs. (**A**) Green, *T. waikamoi*. (**B**) Maroon, *T. kamakou*. (**C**) Small brown, *T. kukuhaa*. (**D**) Large brown, *T. quasimodo*. [Photos: (A), W. Haines; (B to D), R.G.]
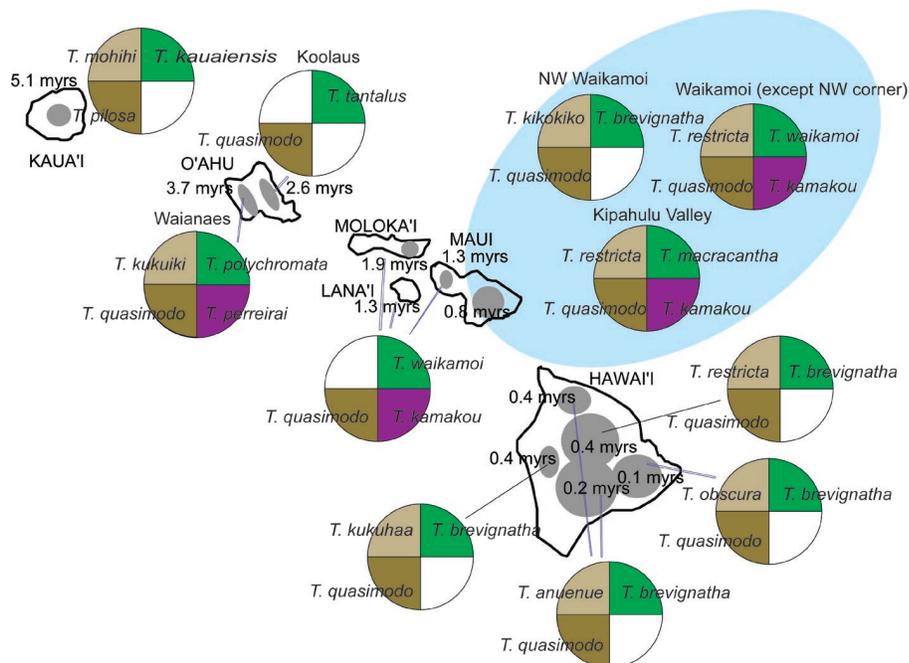

Fig. 2. Ecomorphs in different habitats. Volcanoes are represented by gray circles, with age indicated in millions of years (myrs). Each section of a pie represents a different ecomorph whenever a morph is present at a site: green ecomorph (green), maroon ecomorph (maroon), large brown ecomorph (dark brown), and small brown ecomorph (light brown). Never are two species that share the same ecomorph found in the same locality. This distribution cannot be explained by chance. If the frequency of each ecomorph is assumed to be 25% and if species are distributed randomly among the 12 locations (volcanoes) in similar samples of two, three, or four spider species per locality, then the probability of not finding two species with the same ecomorph at a given locality is extremely small ($P < 10^{-6}$). If the frequency of each ecomorph is estimated from the observed frequency of each, this probability is even more extreme ($P < 10^{-7}$).

although it is ubiquitous, it is mostly represented by a single species, *T. quasimodo*, now found in many habitat types from Oahu to Hawaii. *T. quasimodo* is inferred to have originated on Oahu, independently from the large brown ecomorph on Kauai (*T. pilosa*). Thus, ecomorphs have originated within habitats by two mechanisms: (i) in situ evolution of one ecomorph from another, and (ii) dispersal of an ecomorph from one locality to another with or without speciation.

The similarity of ecomorphs, often with independent origins on different islands, parallels similar observations of other adaptive radiations. Extensive within-locality proliferation and repeated evolution of similar ecomorphs in different localities has occurred in cichlid fish in the African Great Lakes (*12*), sticklebacks in Canadian glacial lakes (*13*), and *Anolis* lizards in the Caribbean (*7*). For the lineage of spiny leg *Tetragnatha*, the phylogenetic analysis also shows progression down the island chain from the oldest (Kauai) to the youngest (Hawaii) island. This is a common feature of most of the Hawaiian taxa that initially colonized the is-

lands ≥5 Ma (*14*, *15*). Because the spiders have diversified within islands, each island displays a series of small adaptive radiations of spiders that reflect time periods dating from 5 Ma to the present. These historical snapshots provide insight into the assembly of species in a community over evolutionary time.

Comparison of patterns of species composition on the youngest Hawaiian island to the oldest shows that the adaptive radiation is dynamic. The most recent stage, as exemplified on the youngest island, is not representative, with only three species of spiny leg *Tetragnatha* endemic to Hawaii Island; the remaining three are shared with East Maui. This distribution might suggest that, over time, these Hawaii Island populations would diverge in allopatry from conspecifics on Maui, with each ecomorph on Hawaii unchanged from its closest relative on Maui. However, this prediction is not supported by observations from older islands, where single colonizations resulted in species proliferation (e.g., one colonization event gave rise to at least five species on Maui and three species on Oahu), and ecomorphs

have evolved largely independently within islands (Fig. 3).

After Hawaii Island, East Maui illustrates the next stage in the chronology of adaptive radiation. Here, a large number of species (multiples of the same ecomorph) exist in allopatry on this relatively young (formed 0.8 Ma) volcano, suggesting that, at least initially, there may be no limit to the number of species that can form subsequent to successful colonization of a given land mass. Considering the situation on Hawaii and Maui together, species accumulation in the initial stages of adaptive radiation seems to involve a "race" between in situ evolution of species, coupled with change in ecomorph type, and dispersal from older islands and subsequent speciation in allopatry without change in ecomorph type. This scenario implies that when population numbers are low (as they are during colonization of new habitats), competition among species is minimal, and there is little impediment to the accumulation of more species. The different older islands each have similar numbers and ecological sets of species, perhaps because of competition after accrual of species. In other words, the community may undergo fine tuning after initial species proliferation, as a result of inter- and intraspecific competition for resources (*16*). Such a process has also been proposed to explain numbers of species in a radiation of weevils in an isolated sub-Antarctic archipelago (*17*).

A markedly similar pattern of species build-up and subsequent decline was observed in ecological studies of mangrove islets off the Florida
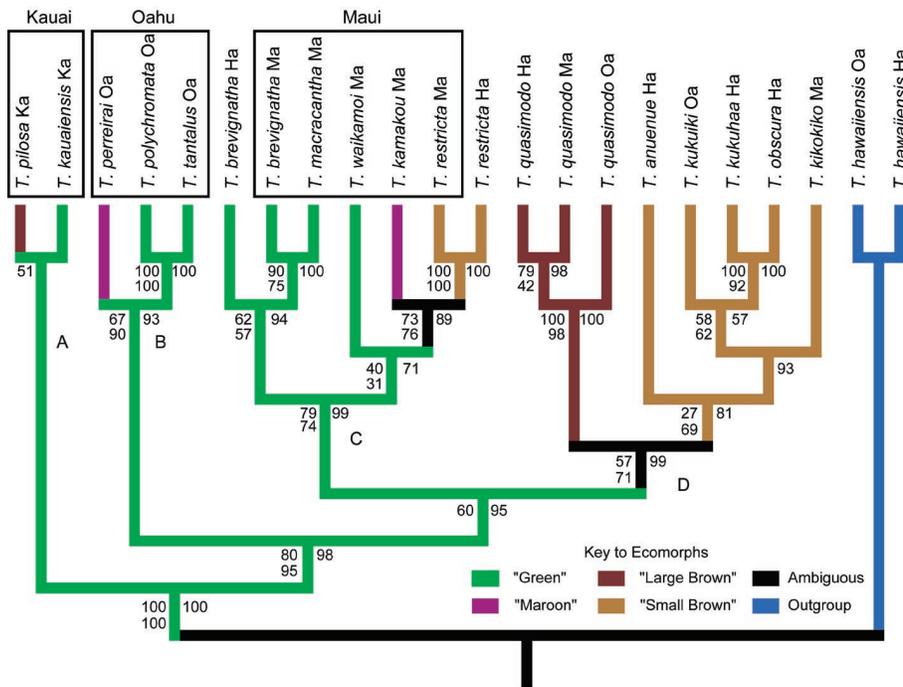

Fig. 3. Phylogeny of the spiny leg clade based on combined mitochondrial cytochrome oxidase I, 12S ribosomal DNA, and 16S ribosomal DNA, and multiple nuclear loci (allozymes) (*20*). Populations of *T. hawaiensis*, a sister species to the spiny leg clade (*11*) also endemic to the Hawaiian Islands, were used as outgroups. The mitochondrial data sets were combined for a total of 1481 base pairs. Phylogenies were reconstructed with maximum parsimony (tree length 1197 steps and consistency index 0.560), distance, and Bayesian inference of likelihood. Bootstrap values >40% are shown on the left of each node, for (top) maximum parsimony and (bottom) distance. Posterior probabilities for the Bayesian tree are shown on the right of each node. Both accelerated and delayed transformation optimization options were applied; colors trace ecomorph state through the tree. For allozymes, a Wagner tree using modified Roger's distance showed the same sister-taxon relationships within each of the major clades marked A, B, C, and D. Islands are indicated for groups that have diversified within an island. To determine whether the species that were similar in ecology and morphology could be monophyletic, each of the four groups (green, maroon, large brown, and small brown) was sequentially constrained to monophyly. Constrained trees were all significantly longer than observed trees (*P* < 0.001). Ka, Kauai; Oa, Oahu; Ma, Maui; Ha, Hawaii.
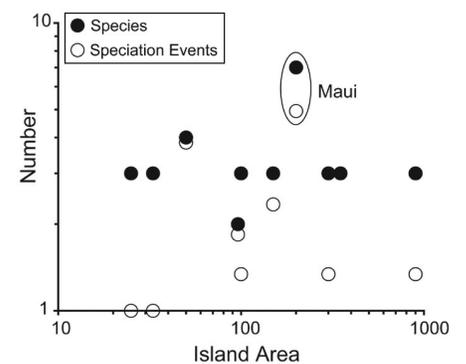

Fig. 4. Species-area relationship. Estimates of area for each volcano were assessed with only the extent of native habitat available; native spiders are confined to such areas, as are most native Hawaiian arthropods (*21*). The size of these forest areas was determined with maps, generated for Hawaiian forest birds (*22*), that cover the 11 volcanoes studied here. Circled points represent East Maui. Variation in ln(area) and island age did not explain variation in either ln(species number) nor ln(inferred speciation events) (multiple regressions, *P* < 0.95 and *P* < 0.44, respectively).

Keys (*18*). After defaunation, species recolonized rapidly. However, rather than gradually climbing to equilibrium, numbers rose in excess of the equilibrium and then declined (*19*), indicating that at low numbers the environment can support more species than at equilibrium. When equilibrium was reached, the species composition was not a random set of species, but rather constituted certain sets of co-adapted species.

An alternative hypothesis accounting for the changes I observed in species numbers across the Hawaiian Islands is that, rather than the stage of an island in community formation through adaptive radiation, it is island size or geological age that determines the number of species or rates of speciation. However, there was no evidence for either of these effects (Fig. 4).

This study of adaptive radiation of Hawaiian *Tetragnatha* spiders shows the dynamic nature of community assembly through adaptive radiation. The chronological arrangement of the islands reveals species accrual over time through both convergent evolution and dispersal, with species numbers highest on a volcano of intermediate age (East Maui). The results mirror those of ecological studies of community assembly and equilibrium theory (*18*). In particular, (i) similar ecological sets of species are formed on each island, and (ii) the pattern of species accumulation through evolution is analogous to that produced solely through immigration on less remote islands, with species numbers increasing to exceed an equilibrium and subsequently declining. Therefore, numbers of species within communities on remote islands are similar to those predicted on the basis of ecological principles elsewhere, where communities arise solely through immigration. In the Hawaiian Islands, species of spiny leg *Tetragnatha* spiders accumulate through both immigration and in situ speciation, with numbers climbing beyond equilibrium and then declining, but in such a manner as to leave a set of nonrandomly associated ecomorphs on any land mass (i.e., no more than one of each at any given location). Because ecological and evolutionary processes of species buildup lead to fundamentally similar outcomes, the study suggests that universal principles may underlie the process of community assembly.

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Defining the Epithelial Stem Cell Niche in Skin

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Many adult regenerative cells divide infrequently but have high proliferative capacity. We developed a strategy to fluorescently label slow-cycling cells in a cell type–specific fashion. We used this method to purify the label-retaining cells (LRCs) that mark the skin stem cell (SC) niche. We found that these cells rarely divide within their niche but change properties abruptly when stimulated to exit. We determined their transcriptional profile, which, when compared to progeny and other SCs, defines the niche. Many of the >100 messenger RNAs preferentially expressed in the niche encode surface receptors and secreted proteins, enabling LRCs to signal and respond to their environment.

Epidermis and its appendages undergo continuous renewal and maintain reservoirs of multipotent SCs whose descendants are organized spatially and temporally. The epidermal basal layer (BL) contains putative SCs in addition to the transiently amplifying (TA) cells, which give rise to terminally differentiating suprabasal layers (*1–3*). The BL and the hair follicle outer root sheath (ORS) are contiguous and biochemically similar (fig. S1A). In the hair bulb, the dermal papilla (DP) maintains contact with matrix TA cells until they differentiate to form the inner root sheath (IRS) and hair shaft. Follicles periodically undergo cycles of growth (anagen), destruction (catagen), and rest (telogen). The zone between noncycling and cycling segments is a SC niche, the ORS "bulge" (*4*, *5*).

Multipotent epithelial SCs with high proliferative potential reside in the bulge (*6*, *7*). The bulge contains the majority of infrequently cycling, label-retaining cells (LRCs), which can respond to anagen DP signals to regenerate the follicle. After wounding or transplantation, bulge cells give rise to epidermis, follicles, and sebaceous glands. Additionally, when dissected from rat whiskers and cultured, bulge cells yield more colonies than other follicle segments (*7*).

It is not known what features define this specialized SC niche, what its interactions with bulge LRCs are, and whether all LRCs are SCs. To begin to address these issues, we devised a strategy based on the prediction that bulge SCs are uniquely both slow-cycling and active for a keratinocyte-specific promoter. With this strategy, we purify and characterize bulge LRCs and related keratinocyte progeny in the BL and ORS. Analyses of their transcriptional profiles reveal the skin LRC mRNAs; some of these mRNAs are found in SCs of other tissues, whereas others specify the unique environment of the skin SC niche.

To mark infrequently cycling cells of adult skin epithelium, we engineered transgenic mice to express histone H2B–green fluorescent protein (GFP) (*8*) controlled by a tetracycline-responsive regulatory element (TRE). A tightly regulated TRE-mCMV-H2B-GFP founder animal was crossed with mice harboring a keratin 5 (K5) promoter–driven tet repressor–VP16 transgene (*9*), and offspring were selected for doxycycline (Tet)–controlled regulation restricted to skin epithelium (Fig. 1A). Without Tet, backskin

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