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The involvement of weakly adsorbed water in multiple mechanistic steps is also consistent with the large reaction order (1.3). DFT calculations also indicate that a second adsorbed water molecule in the vicinity of the *COOH species facilitates the proton transfer, which only needs to overcome the thermodynamic barrier (ΔE = 0.70 eV, E_a = 0.70 eV, SM 6.6). Further, at higher water coverage, rapid proton mobility (33) can explain the shift to an equilibrium isotope effect. *COOH decomposition has also been identified as the RDS in the related WGS reaction on Cu and Pt (34, 35), and this elementary step is consistent with reports of NaOH promoting CO oxidation over Au catalysts (17, 36).

The CO oxidation mechanism shown in Fig. 4, along with the structural model of support OH groups anchoring and activating water near Au particles, provides a fresh framework for interpreting previous results. This model provides a single active-site description that unifies some very disparate mechanistic information, accounts for the promotional effects of water, and is consistent with previously reported isotope exchange studies (21, 27) that indicate that CO and O_2 must react directly on the Au particles without exchanging O atoms with the support or adsorbed water. At the same time, it maintains the importance of the support OH groups and the metal-support interface without directly involving them in the reaction mechanism. The likely active sites bear a strong resemblance to the WGS mechanism over Au catalysts, where the support anchors water near Au-CO sites (6).

This proposed mechanism explains why the O_2 adsorption and activation steps, which are widely regarded as the critical mechanistic steps, have been so difficult to characterize. The fast room-temperature catalysis mechanism requires both water and CO for O_2 binding and activation. Experiments performed without water, particularly ultrahigh-vacuum and DFT studies, ultimately probe different reaction mechanisms than what appears to be the dominant room-temperature pathway on supported catalysts. Similarly, most traditional catalyst studies rarely control or report feedwater contents, which has likely contributed to the wide range of reported CO oxidation activities for Au/TiO_2 catalysts and to the difficulties in understanding the key features of the best catalysts. Finally, this new mechanism brings the interpretation of traditional supported catalyst experiments more in line with computational and surface-science studies, which have largely indicated that the key reaction steps occur on Au (7, 9–14, 17, 29), without direct participation of the support.

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PLANT ECOLOGY

Environmental filtering explains variation in plant diversity along resource gradients

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The mechanisms that shape plant diversity along resource gradients remain unresolved because competing theories have been evaluated in isolation. By testing multiple theories simultaneously across a >2-million-year dune chronosequence in an Australian biodiversity hotspot, we show that variation in plant diversity is not explained by local resource heterogeneity, resource partitioning, nutrient stoichiometry, or soil fertility along this strong resource gradient. Rather, our results suggest that diversity is determined by environmental filtering from the regional flora, driven by soil acidification during long-term pedogenesis. This finding challenges the prevailing view that resource competition controls local plant diversity along resource gradients, and instead reflects processes shaping species pools over evolutionary time scales.

For decades, ecologists have sought to understand patterns in terrestrial plant diversity along environmental gradients (1). Prominent theories emphasize resource competition as a key driver of diversity (2–4). Alternatively, it has been proposed that variation in local plant diversity along gradients reflects the filtering of species that are poorly adapted to local environmental conditions (5–7), highlighting the importance of long-term evolutionary processes in shaping species pools and present-day patterns of plant diversity. These competing hypotheses have been considered in isolation, and further progress can be made only by considering the

multivariate links between resource supply, species pools, and local plant diversity (8).

To disentangle how resource supply and species pools interact to control local plant diversity, we studied a >2-million-year coastal dune chronosequence near Jurien Bay in southwestern Australia (30°01′ to 30°24′S; 114°57′ to 115°11′E) (9) (also see supplementary materials and methods). The chronosequence provides a distinctive opportunity to explore controls over local plant diversity for several reasons (10). First, the broad range in soil age leads to an exceptionally strong natural gradient in nutrient availability and stoichiometry while minimizing variation in other important ecosystem factors such as climate, topography, and parent material (9, 11). Additionally, the fact that all chronosequence stages are found within a short (~10-km) distance ensures that differences in species pool sizes among stages can be due to environmental filters only, thus ruling out dispersal limitation as a causal factor. Further, previous studies showed that nutrient availability strongly constrains plant growth along the chronosequence (9, 11), whereas the open canopy of the shrubland vegetation (average leaf area index <0.5) rules out light as a limiting resource. Finally, the chronosequence is located in one of the most floristically diverse regions on Earth (12), enabling us to further our understanding of the controls over plant diversity in species-rich ecosystems.

We evaluated prominent hypotheses about how local soil resources might drive local plant diversity along this resource gradient (10) (Fig. 1). First, spatial heterogeneity in soil properties might allow more niches for species with different resource requirements to coexist locally (13, 14). Second, plant diversity might show a unimodal ("hump-shaped") response to soil fertility, declining under higher fertility due to competitive exclusion (2, 4). Third, plant diversity might be greatest where no single soil nutrient strongly limits plant growth (i.e., colimitation) if species show trade-offs in their ability to acquire different nutrients (15). Here, we focus on nitrogen (N) and phosphorus (P) because these are the two nutrients that most strongly limit or colimit plant growth along this chronosequence (9, 11). Fourth, a greater diversity in the forms of N or P present in soils might promote plant diversity through resource partitioning, if species differ in their preference for different forms of these nutrients (16, 17). Finally, variation in plant diversity along resource gradients might simply reflect environmental filtering from the regional flora due to key abiotic properties (e.g., soil pH or total [P]), thus leading to species pools of varying sizes, with no need to invoke factors that might influence resource competition (5–7, 18) (Fig. 1).

To test these hypotheses, we studied vegetation and soils from 60 permanent 10-by-10–m

plots encompassing six chronosequence stages (i.e., 10 replicate plots per stage) for which soils ranged in age from the present day (stage 1) to >2 million years old (stage 6) (9). In each plot, we measured species composition, density, and canopy cover of all vascular plants. We use rarefied plant species richness as our measure of local plant diversity, thus controlling for differences in plant density (fig. S1) or sampling effort (19). We collected seven surface (0 to 20 cm) soil samples per plot and determined pH and a range of soil nutrients. We also collected leaf samples and analyzed them for nutrients (11). Finally, we grew canola (*Brassica napus*) in soils collected from each plot to derive a plant-based index of soil fertility.

To determine the relative importance of soil resource factors and species pool effects on local plant species richness, we translated our conceptual causal model (Fig. 1) into one that could be evaluated quantitatively (10). The resulting structural equation model (Fig. 2A) was well supported by the data (χ^2 = 40.1, df = 42, P = 0.555), and none of the independence claims implied by the model were statistically significant (P > 0.05), suggesting that all of the important relationships were specified in the model. As expected from previous results (9, 11), long-term pedogenesis led to strong shifts in the local soil resource factors that have been hypothesized to influence plant species richness, either directly or indirectly via declines in soil total P and pH (Figs. 2 and 3A). However, despite the marked changes in soil resources along the chronosequence, variation in local plant species richness was explained almost entirely by soil pH (Figs. 2A and 3C). By contrast, there were no significant effects on local plant species richness of soil spatial heterogeneity, N:P stoichiometry, or diversity of N and P forms (Fig. 2A), although species richness showed a weak but statistically signifi-

cant hump-shaped relationship with soil fertility after accounting for all other factors (fig. S2). Still, adding local soil resource factors as predictors to a model that considered only soil pH provided a worse fit to the data [model with only soil pH as predictor: Akaike's information criterion (AIC) = 353; model with soil pH and all local resource factors presented in Fig. 2A as predictors: AIC = 360; likelihood-ratio test: L = 10.1, df = 9, P = 0.344], reinforcing the importance of soil pH as a causal factor.

To determine whether the effect of soil pH on local species richness was the result of environmental filtering from the regional flora, we estimated the species pool size for each chronosequence stage (fig. S3) using the second-order jackknife estimator (20) and included this variable in a second model (Fig. 2B). This model was well supported by our data (χ^2 = 48.6, df = 58, P = 0.804) and showed that the negative effect of soil pH on local plant diversity could be explained by environmental filtering from the regional flora (Figs. 2A and 3, C to E).

Our results thus reveal that environmental filtering from the regional flora is the dominant factor explaining variation in local plant diversity along this strong resource gradient, overriding factors associated with local resource competition that have been the focus of several prominent theories. A negative effect of high soil pH on local plant diversity is expected in regions where acidic soils have been common throughout evolutionary history (18). Accordingly, the species-rich flora of southwestern Australia has evolved predominantly on ancient, strongly weathered and, therefore, acidic soils (12). One explanation underlying the negative effect of high pH on plant diversity is a poor capacity of many plant species to acquire micronutrients or P from calcareous soils (21). However, although pH best explained variation in the size of species pools along this
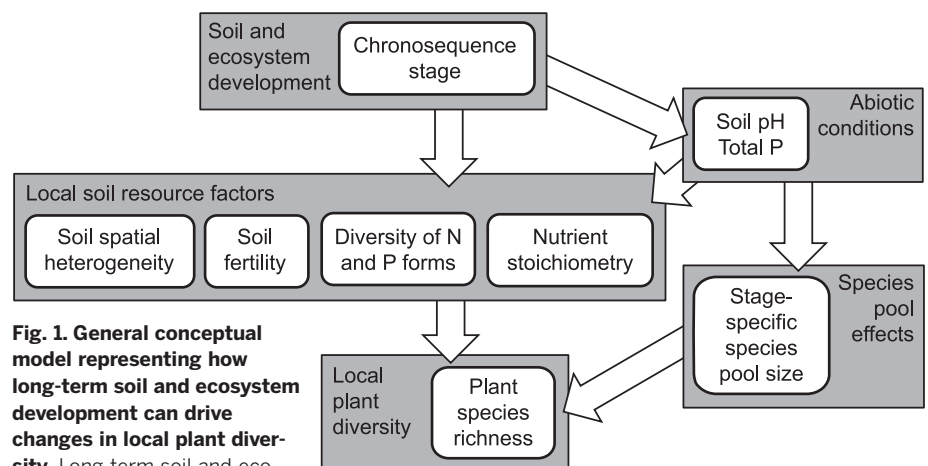

Fig. 1. General conceptual model representing how long-term soil and ecosystem development can drive changes in local plant diversity. Long-term soil and ecosystem development (here represented by "chronosequence stage") can lead to changes in the local soil resource factors that prominent theories emphasize as key drivers of local plant diversity along resource gradients (10). In addition, pedogenesis leads to changes in abiotic conditions such as soil P concentrations and pH, which can also affect those local soil resource factors (10). Finally, abiotic conditions such as pH can lead to environmental filtering from the regional flora to give rise to stage-specific species pools of varying sizes, which can influence local plant diversity through proportional sampling (6).

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gradient (Fig. 2B), we note that pH and soil total [P] are strongly correlated (correlation coefficient $r = 0.97$, $P < 0.0001$) (fig. S4). As such, it is possible that environmental filtering from the regional flora along this gradient reflects P toxicity on P-rich soils in species adapted to infertile conditions (21) and, conversely, inefficient use of P on P-impoverished soils in species adapted to fertile conditions (11).

For completeness, we also tested the effect of individual soil resource factors on local plant diversity separately to explore whether some of these effects could have been deemed significant had the influence of pH and species pools not been appropriately considered (i.e., not included in the models). When tested independently, both the diversity of P forms and leaf N:P ratio showed positive and significant ($P < 0.05$) effects on local plant diversity (table S1), which could have been interpreted as a role for P partitioning (17) or greater plant diversity under P limitation (22). However, both of these effects disappeared once variation in soil pH and species pool sizes among chronosequence stages were taken into account (Fig. 2).

The importance of evolutionary or biogeographical history in shaping floras to explain global patterns of plant diversity (e.g., the latitudinal gradient of plant diversity) has long been recognized (23). However, species pools have received less attention (6) than resource competition (2, 3) as explanations for patterns of plant diversity along local resource gradients. Although previous studies have highlighted the importance of environmental filtering and species pools in explaining local plant diversity patterns (7, 24–27), our study provides the strongest support to date for this hypothesis by simultaneously evaluating prominent theoretical predictions about the role of soil resources in driving local plant diversity (10)—namely those associated with spatial resource heterogeneity (13, 14), resource partitioning (16, 17), nutrient stoichiometry (3, 15), and soil fertility (2, 4). Our finding that environmental filtering from the regional flora is the dominant driver of local plant diversity along this resource gradient is important because our design allows us to rule out dispersal filters while minimizing variation in ecosystem properties (e.g., climate, soil texture, topography, parent material) that can amplify species pool effects. That said, the relatively low productivity and frequent disturbance by fire, coupled with a species-rich flora, might partly explain the strong species pool effects over local plant diversity in this system (28). Further research should explore whether local resource factors become more important in more productive and less frequently disturbed systems, as well as in less species-rich systems.

An improved mechanistic understanding of the controls over terrestrial plant diversity is critical for predicting how diversity may respond to environmental change (29, 30). Overall, our study supports the view that local plant diversity patterns along resource gradients cannot be understood without considering the interaction between evolutionary history and local abiotic
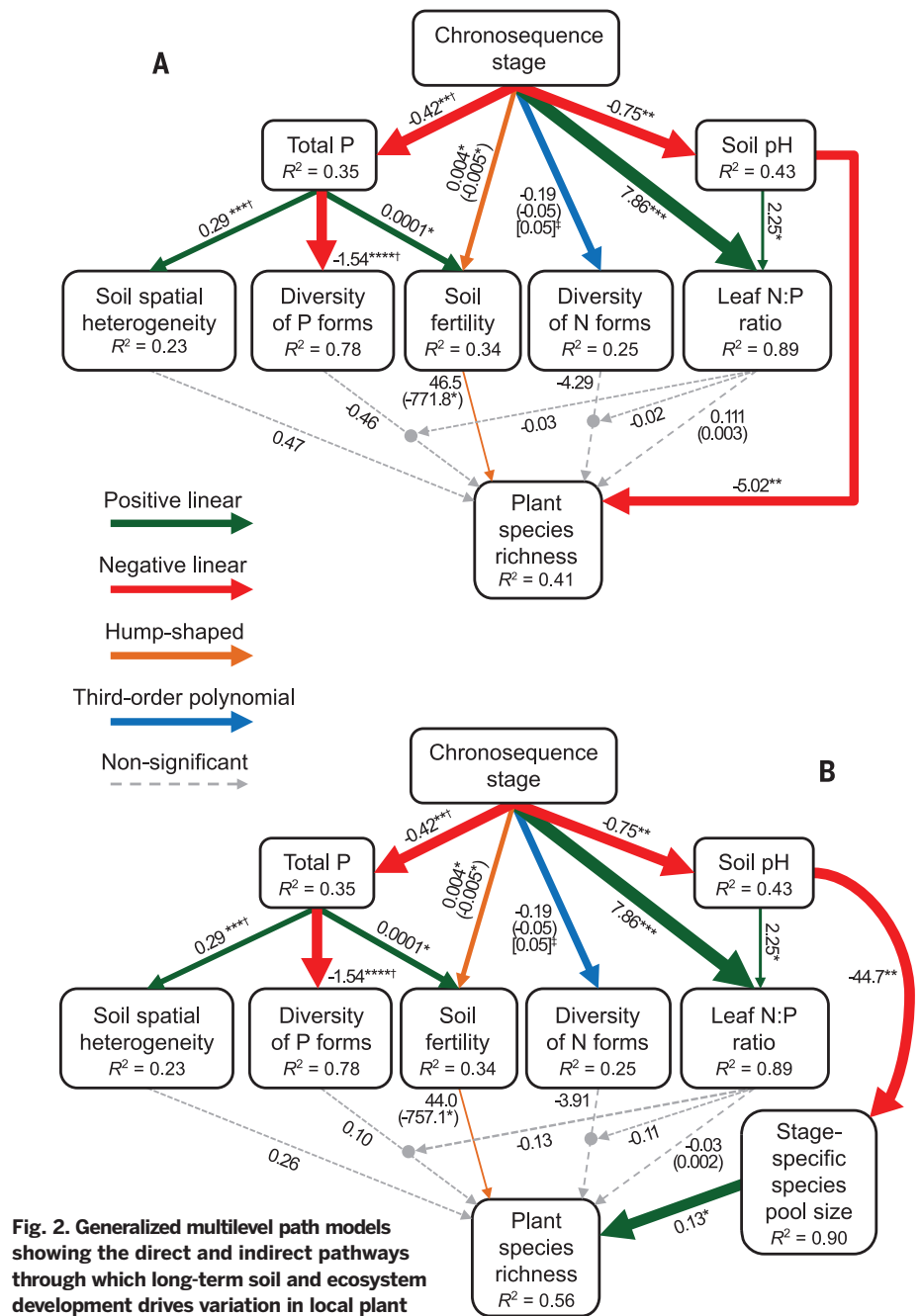

Fig. 2. Generalized multilevel path models showing the direct and indirect pathways through which long-term soil and ecosystem development drives variation in local plant species richness. (**A**) Model with direct link from soil pH to local plant species richness. (**B**) Model with effect of soil pH on local plant species richness mediated via changes in the size of each stage-specific species pool. Rarefaction was used to remove effects of plant density on species richness. Arrows represent the flow of causality. Arrows pointing to other arrows represent interactive effects, whereby one variable is expected to influence the strength and direction of the relationship between two other variables. Both models were well supported by our data [(A): $\chi^2 = 40.1$, df = 42, $P = 0.555$; (B): $\chi^2 = 48.6$, df = 58, $P = 0.804$], and none of the independence claims implied by the model were statistically significant at $\alpha = 0.05$. Path coefficients (i.e., numbers associated with each arrow) are unstandardized regression coefficients. Arrow width is proportional to the standardized path coefficient and can be interpreted as the relative importance of each factor. For nonlinear relationships involving polynomial terms, path coefficients for second-order polynomials are shown in parentheses, whereas those for third-order polynomials are in shown in square brackets. Standardized path coefficients for nonlinear relationships involving polynomial terms were computed using composite variables. Statistical significance for nonlinear relationships was tested using likelihood-ratio tests. Gray dashed arrows represent nonsignificant ($P > 0.05$) relationships. †Total phosphorus (P) was log-transformed in these analyses. ‡$0.05 < P \le 0.1$; *$P \le 0.05$; **$P \le 0.01$; ***$P \le 0.001$; ****$P \le 0.0001$. N, nitrogen. R^2, coefficient of determination.
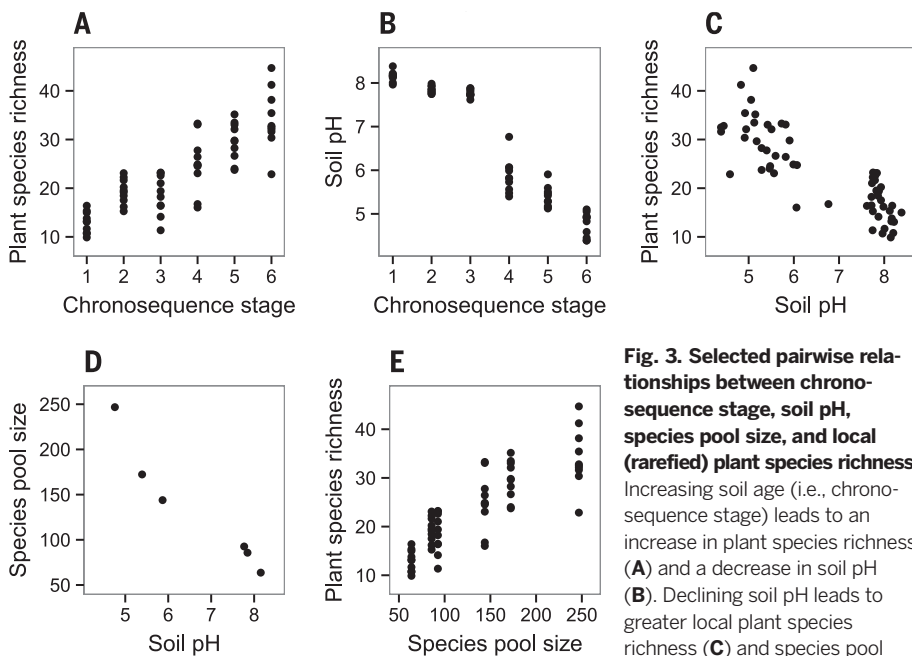
Fig. 3. Selected pairwise relationships between chronosequence stage, soil pH, species pool size, and local (rarefied) plant species richness. Increasing soil age (i.e., chronosequence stage) leads to an increase in plant species richness (**A**) and a decrease in soil pH (**B**). Declining soil pH leads to greater local plant species richness (**C**) and species pool sizes (**D**). Local plant species richness is greater with larger species pools (**E**). In (D), there are only six data points (i.e., one per chronosequence stage) because species pool size was estimated for each stage.

conditions (5, 6). Moreover, it suggests that the prevailing view by which mechanisms associated with local resource competition best explain patterns in local plant diversity along resource gradients should be revisited (6). Our results do not imply that local resource factors and niches are unimportant in promoting local plant species coexistence within individual communities (31); rather, they suggest that such factors may not explain variation in plant diversity among communities. Our finding about the importance of environmental filtering and species pools in shaping local plant diversity patterns along resource gradients might also help to explain why studies find inconsistent responses of plant diversity to productivity (8).

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PLANT DEVELOPMENT

Direct roles of SPEECHLESS in the specification of stomatal self-renewing cells

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Lineage-specific stem cells are critical for the production and maintenance of specific cell types and tissues in multicellular organisms. In *Arabidopsis*, the initiation and proliferation of stomatal lineage cells is controlled by the basic helix-loop-helix transcription factor SPEECHLESS (SPCH). SPCH-driven asymmetric and self-renewing divisions allow flexibility in stomatal production and overall organ growth. How SPCH directs stomatal lineage cell behaviors, however, is unclear. Here, we improved the chromatin immunoprecipitation (ChIP) assay and profiled the genome-wide targets of *Arabidopsis* SPCH in vivo. We found that SPCH controls key regulators of cell fate and asymmetric cell divisions and modulates responsiveness to peptide and phytohormone-mediated intercellular communication. Our results delineate the molecular pathways that regulate an essential adult stem cell lineage in plants.

In multicellular organisms, the need to generate and maintain diverse cell types and tissues is fulfilled by lineage-specific stem cells (*1*). These stem cell lineages, active postembryonically, produce a defined set of cell types. Although the origins of these lineage-specific stem cells during development are largely obscure, master transcription factors are implicated in their specification in both animals and plants (*1–3*).

However, low expression levels and/or presence in a limited number of cells makes genome-wide study of these transcriptional regulators by standard chromatin immunoprecipitation (ChIP) assays, the most common technique for studying protein-DNA interactions, technically challenging.

Stomata are epidermal valves that mediate gas exchange between the plant and atmosphere. In *Arabidopsis*, stomatal guard cells are derived