

UNIVERSIDADE FEDERAL DA BAHIA  
INSTITUTO DE BIOLOGIA  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA: TEORIA, APLICAÇÃO E  
VALORES

**LISTA DE ARTIGOS REFERENTES AO PROCESSO SELETIVO (PROVA DE  
FORMAÇÃO CIENTÍFICA) PARA INGRESSO DE NOVOS ALUNOS DO PROGRAMA  
DE PÓS-GRADUAÇÃO EM ECOLOGIA: TEORIA, APLICAÇÃO E VALORES  
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As questões referentes à prova de formação científica serão baseadas em 4 (quatro) artigos científicos (citados abaixo e em anexo nesse documento). A comissão ressalta que as questões da prova incluirão conhecimentos gerais ligados as teorias abordadas nos artigos. Assim, recomenda-se que os candidatos complementem seus estudos em outras fontes bibliográficas.

- Carnaval et al. (2009) Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot. *Science* 323: 785-789.
- Rahbek et al. (2019) Building mountain biodiversity: Geological and evolutionary processes. *Science* 365: 1114-1119.
- Smith & Tinker (2022) Alternations in the foraging behaviour of a primary consumer drive patch transition dynamics in a temperate rocky reef ecosystem. *Ecology Letters* 25: 1827-1838.
- Strauss & Shizuka (2022) The ecology of wealth inequality in animal societies. *Proc. R. Soc. B* 289: 20220500.

## LETTER

# Alternations in the foraging behaviour of a primary consumer drive patch transition dynamics in a temperate rocky reef ecosystem

Joshua G. Smith<sup>1,2</sup>  | M. Tim Tinker<sup>1</sup> <sup>1</sup>Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California, USA<sup>2</sup>National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California, USA**Correspondence**Joshua G. Smith, Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, 115 McAllister Way, Santa Cruz, CA 95060, USA.  
Email: [joshsmith@nceas.ucsb.edu](mailto:joshsmith@nceas.ucsb.edu)**Funding information**

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**Abstract**

Understanding the role of animal behaviour in linking individuals to ecosystems is central to advancing knowledge surrounding community structure, stability and transition dynamics. Using 22 years of long-term subtidal monitoring, we show that an abrupt outbreak of purple sea urchins (*Strongylocentrotus purpuratus*), which occurred in 2014 in southern Monterey Bay, California, USA, was primarily driven by a behavioural shift, not by a demographic response (i.e. survival or recruitment). We then tracked the foraging behaviour of sea urchins for 3 years following the 2014 outbreak and found that behaviour is strongly associated with patch state (forest or barren) transition dynamics. Finally, in 2019, we observed a remarkable recovery of kelp forests at a deep rocky reef. We show that this recovery was associated with sea urchin movement from the deep reef to shallow water. These results demonstrate how changes in grazer behaviour can facilitate patch dynamics and dramatically restructure communities and ecosystems.

**KEY WORDS**

alternative stable states, behaviour, kelp forest, patch dynamics, trophic cascades

## INTRODUCTION

The importance of behaviour in linking individuals to ecosystems is widely recognised in the ecological literature (Ovadia & Schmitz, 2002; Schmitz, 1998; Sih et al., 2012; Werner & Peacor, 2003). Behaviour can facilitate community structure and functioning by altering the relative influence of key species interactions (e.g. competition, predation, mutualisms), changing the distribution of resources and through other non-consumptive response pathways (Estes et al., 1998; Pace et al., 1999; Werner & Peacor, 2003). Although the debate continues over the relative importance of density versus behaviorally mediated influences of predators and primary consumers, both occur widely in nature and are often associated with trophic cascades (Beckerman

et al., 1997; Kauffman et al., 2010; Schmitz et al., 1997; Werner & Peacor, 2003). Therefore, understanding how the presence of predators and resource availability reciprocally influence the behaviour of primary consumers is central to advancing knowledge of community structure, functioning, stability, and transition dynamics.

Sea urchin grazing in marine ecosystems around the world is often considered a fundamental driver of shifts from algal-dominated habitats to alternative sea urchin 'barrens' that are void of macroalgae (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015). These shifts have profound consequences on the structure and functioning of coral reefs, seagrass, kelp forest and rocky intertidal ecosystems (Done, 1992; Filbee-Dexter & Scheibling, 2014; Watson & Estes, 2011). Resource availability and predator-driven impacts are perhaps the two

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most well-documented factors known to influence patterns in sea urchin grazing behaviour (Burt et al., 2018; Cowen, 1983; Harrold & Reed, 1985; Mann, 1982). Cascading effects resulting from the loss of sea urchin predators provide strong evidence of density-mediated indirect interactions (Burt et al., 2018; Estes et al., 1998), whereas reductions in the availability of food or risk-cues have been associated with behaviorally mediated indirect interactions (Harding & Scheibling, 2015; Spyksma et al., 2017). However, the relative influence of these factors is often context-dependent and difficult to decouple from other more environmentally driven processes such as how grazers respond to substrate complexity, seasonality, swell and water temperature (Konar et al., 2014; Randell et al., 2022; Vivian-Smith, 1997). Therefore, the factors that contribute to modifications in sea urchin grazing behaviour can have important implications for the state of communities and ecosystems.

In temperate kelp forest ecosystems, sea urchin behaviour can be categorised into two fundamental modalities. In kelp forests, where abundant detrital (i.e. 'drift') algae are deposited in crevices, urchins mainly employ a cryptic passive-grazing modality (Duggins et al., 1989; Krumhansl & Scheibling, 2012; Sala & Zabala, 1996). The presence of predators may also elicit a direct response in sea urchins that influence cryptic behaviour or indirectly by maintaining forests (and therefore abundant drift) through trophic cascades (Cowen, 1983; Estes et al., 1998). However, when the production of detrital kelp is limited, sea urchins fundamentally shift their behaviour to an active grazing modality, where they emerge from the refuge and roam on an open reef surface in search of live macroalgae (Harrold & Reed, 1985; Kriegisch et al., 2019). Additionally, because sea urchins have a dispersive larval-stage life history, kelp-urchin dynamics can also be strongly driven by spatially explicit and episodic recruitment (Lafferty & Kushner, 2000; Okamoto et al., 2020).

Kelp forests along the west coast of North America recently experienced a rapid and pronounced shift from highly expansive forests to unproductive sea urchin barrens. Starting in late 2013, a coast-wide sea star epizootic decimated the urchin predator *Pycnopodia helianthoides* (hereafter, *Pycnopodia*), followed by an episodic marine heatwave event that occurred from mid-2014 into 2016 (Harvell et al., 2019; McPherson et al., 2021). Shortly after (2014–2016), large-scale reductions in kelp biomass were recorded along the mainland coasts of California, the United States and Baja California, Mexico (Beas-Luna et al., 2020), with pronounced urchin outbreaks occurring in central and northern California (McPherson et al., 2021; Smith et al., 2021). In northern California where bull kelp (*Nereocystis luetkeana*) is the dominant structure-forming foundation species, over a 95% reduction in historical kelp biomass was documented (McPherson et al., 2021; Rogers-Bennett & Catton, 2019). Similar large-scale loss of kelp biomass was recorded at the southern range

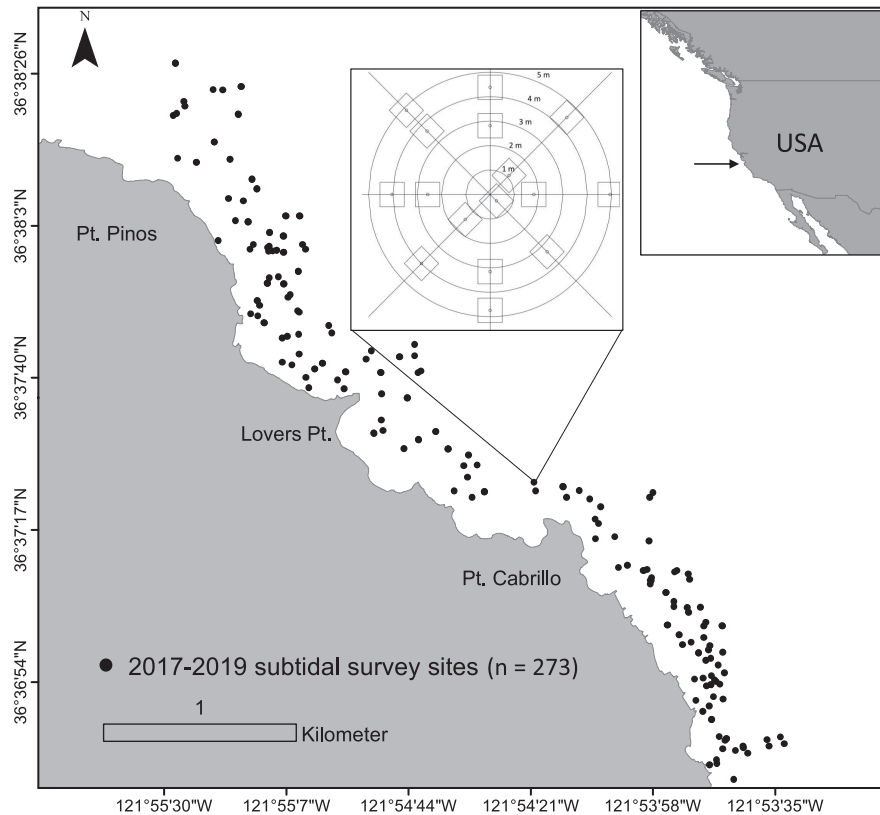
limit of the giant kelp (*Macrocystis pyrifera*) near Bahía Asunción, Mexico (27.1°N; Arafeh-Dalmau et al., 2019; Beas-Luna et al., 2020). However, along the central coast of California, giant kelp-dominated forests experienced a shift to a patchy mosaic of remnant forests interspersed with sea urchin barrens (Smith et al., 2021). As such, whether the observed 2014 sea urchin outbreak resulted from a behavioural shift (i.e. from passive grazing of detrital algae to active grazing on live macroalgae) or from changes in recruitment remains unresolved.

In this study, we explore whether an outbreak of purple sea urchins that occurred in 2014 along the Monterey Peninsula, CA, USA was driven by a behavioural shift (i.e. emergence from refuge or redistribution following the regional extirpation of *Pycnopodia* and reduced productivity of kelp associated with the marine heatwave) or by a demographic response (i.e. changes in survival or recruitment). We then tracked the behaviour of sea urchins in the years following the 2014 outbreak to determine how grazer behaviour shapes alternations between kelp-dominated (hereafter, 'forested') and urchin-dominated (hereafter, 'barren') states. This study was motivated by the following hypotheses: (1) sea urchins emerged from refuge following the regional collapse of *Pycnopodia*, the 2014–2016 marine heatwave, and a decline in kelp production, (2) sea urchin behaviour (passive or active) explains patch state (forested or barren) transition dynamics and (3) sea urchin migration in search of alternative food sources is associated with macroalgae recovery.

## MATERIALS AND METHODS

### Study system

This study was conducted in the nearshore temperate reefs of southern Monterey Bay, California, USA (Figure 1). All marine algae and invertebrates within the survey region are protected from harvest within marine protected areas. The giant kelp, *Macrocystis pyrifera*, is the dominant habitat-forming algae and the purple sea urchin, *Strongylocentrotus purpuratus* (hereafter, 'sea urchin'), is the principal benthic herbivore, although bull kelp (*Nereocystis luetkeana*) and red sea urchins (*Mesocentrotus franciscanus*) also inhabit the region. In 2013, a coastwide sea star wasting syndrome occurred that extirpated the urchin predator *Pycnopodia helianthoides* throughout California by 2014 (Harvell et al., 2019). Shortly thereafter, a dramatic increase in visually detectible sea urchins shifted the region into a patchy mosaic of remnant forests interspersed with sea urchin barrens (Smith et al., 2021). We used long-term benthic subtidal monitoring data to determine whether the initial sea urchin outbreak was primarily evidenced by a behavioural shift or by a demographic response (i.e. sea urchin recruitment or survivorship). We then conducted a series of separate surveys over the course of 3 years to explore whether (and how) sea



**FIGURE 1** Study area along the Monterey Peninsula, California, USA. Each point represents an independent replicate survey site sampled from 2017 to 2019. The inset diagram depicts the sampling design used to survey each site using eight 5-m long transects (lines) radiating from a fixed central position, with two 1 m<sup>2</sup> quadrats (squares) sampled per transect

urchin behaviour is associated with patch state transition dynamics across the mosaic.

### Sea urchin behavioural shifts at the regional scale

To determine the temporal point when the sea urchin outbreak occurred, we conducted change-point analyses on a 22-year time series of published subtidal data collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO; Malone et al., 2021). Briefly, we used all 12 PISCO sites (Figure S1) surveyed annually between mid-June to mid-October from 1999 to 2021 in southern Monterey Bay, California. Annual surveys at each site consisted of visual surveys by SCUBA divers of the density and percent cover of conspicuous benthic algae, invertebrates, and benthic and water column-dwelling fishes. Density and percent cover estimates of conspicuous benthic algae and invertebrates were recorded along with six replicate 2 × 30 m transects stratified across three bottom depths (5, 12.5, 20 m; two transects per depth level). We used a segmented regression with multiple change points to determine the most likely temporal change point locations on the mean transect density (no. per 60 m<sup>2</sup>) of sea urchins surveyed in sequential years.

To determine whether the sea urchin outbreak is explained by a shift in sea urchin behaviour from passive to active grazing, we examined the annual size frequency (test diameter recorded to the nearest 1 cm) of sea urchins recorded on PISCO surveys from 2011 to 2016 (sea urchin sizing began in 2011). Support for the behavioural shift hypothesis would be evidenced by increases in counts of all size classes of urchins as they emerged from crevices and became more visible on surveys. Alternatively, support for the recruitment hypothesis (i.e. that the urchin outbreak was associated with a recruitment event) would be evidenced by a dramatic and disproportionate increase in the frequency of sea urchins less than 3 cm. We used a Kolmogorov–Smirnov test to evaluate equality in urchin size distribution across the critical 2013–2014 breakpoint (identified from the segmented regression). Finally, we tested for a relationship between urchin counts and terrain ruggedness (i.e. reef complexity), reef slope and relief among which we found no effect (Supplementary Information Methods).

### Population state dynamics

To further explore whether the marked increase in counts of adult (>3 cm) sea urchins after 2013 is explicable by a sea urchin behavioural shift, we used a

Bayesian hierarchical framework to fit a size-structured population dynamics model to survey data. We used this model to evaluate sea urchin recruitment, survival (growth) and detection probability as plausible drivers of observed population dynamics. The structure of the process model is described in detail in Supplementary Information Methods. Briefly, the key demographic processes were the annual rates of growth, survival and recruitment, while a fourth observer process (detection probability) related the latent dynamics of the true population to the observed survey data. We assume that detection probability is reflective of sea urchin behaviour (i.e. whether sea urchins are cryptic and not counted on surveys or actively grazing and visible to divers). The model tracked the dynamics of 10 size classes (corresponding to 1 cm size increments), with growth transition probabilities between size classes parameterised from literature-reported values (Ebert, 2010). Model-estimated parameters included baseline values of recruitment, survival and size-specific detection probability as well as year-to-year differences in each of these processes over the study period (1999–2021) that were estimated as hierarchical random effects.

We used standard Markov Chain Monte Carlo methods (MCMC) to fit the process model to survey data on average size-structured urchin counts per transect (details of fitting methods and diagnostics are described in detail in Supplementary Methods). We summarised the estimated proportional changes in recruitment, survival and detection probability after 2013, and we used a simulation-based sensitivity analysis to calculate the relative contribution of variation in each of these processes to the observed increase in urchin counts over the study period.

## Patch-level dynamics

We explored patch-level dynamics over a 3-year study period (2017–2019) using additional field surveys to further examine how sea urchin behaviour underpins switching among patch states (forest, barren). Survey sites were initially randomly selected and sampled annually from May to September in 2017 ( $n = 90$ ), 2018 ( $n = 111$ ) and 2019 ( $n = 72$ ) to determine patch transition dynamics and attributes of each patch state such as sea urchin behaviour, density and the cover of key groups of algae (Figure 1). Survey sites were randomly selected on hard substratum between 5 and 20 m of water (based on diving limitations) and consistent efforts were made to replicate spatial sampling through time (i.e. survey sites were resampled in 2018 and 2019). A site consisted of 16  $1 \text{ m}^2$  quadrats randomly stratified across eight 5-m long transects (two quadrats per transect), and each transect radiated from a fixed central location (Figure 1). Therefore, each survey site represents an independent replicate sample.

The state (barrens, forest) of each site was characterised by constructing a linear discriminant analysis (LDA) using urchin behaviour (density exposed and concealed), density and the percent cover of algae as classifiers. In the field, each site was surveyed using 16 randomly placed  $1 \text{ m}^2$  quadrats fixed with a high-resolution GoPro Hero4 camera and two Sola LED video lights. The density of urchins was recorded in situ within each quadrat by quantifying visually detectible sea urchins and by searching in cracks and crevices for cryptic individuals. We also recorded site patch states (barrens, forest) based on initial impressions of the site at the start of each dive. In the lab, photoquadrats were analysed to determine the number of actively foraging (i.e. exposed) sea urchins and to estimate the cover of key algal groups that are characteristic of forests and barrens. Each photoquadrat was assigned 16 universal points using a digital grid in ImageJ. Because many algae are difficult to visually quantify to the species level in imagery, we used four taxonomic categories that are known indicators of patch state (Filbee-Dexter & Scheibling, 2014): articulated coralline algae, encrusting coralline and red algae, brown algae and foliose red algae. Finally, exposed sea urchins of all detectible sizes were quantified from photoquadrats by counting only urchins where 50% or more of the test diameter was visible (Smith et al., 2021). We then constructed the LDA by using these variables (sea urchin density, proportion of exposed urchins, cover of algae) as predictors of the field patch-state classification. Out of 284 sites used in training the LDA, only seven were misclassified and the entropy  $R^2$  was 0.89. Therefore, we elected to use the predicted states from the LDA (rather than diver-based site impressions) in subsequent analyses.

To test the hypothesis that shifts in patch state are associated with alternations in sea urchin foraging behaviour, we explored transition dynamics across two time steps (2017–2018 and 2018–2019). For this analysis, only sites surveyed at the same spatial location in sequential years were used to determine whether each site (1) persisted in the same state across the time step, (2) forward-shifted from a forest to barren or (3) reverse-shifted from a barren to a forest. Logistic regression was used to determine the transition probability based on the natural log-transformed mean density of exposed (i.e. actively foraging) sea urchins, the mean number of cryptic urchins and starting state (barren, forest). We defined the logistic target level based on a positive state shift, where a transition to a different state in the following year was classified as ‘1’ and state persistence as ‘0’. Therefore, each of the variables in the model represents starting-year values used to predict the following-year state. We used AIC model selection to identify the best-fit relationship between patch transition and the density of sea urchins exposed or concealed. Finally, to determine the strength of discontinuity in state-shift

thresholds, we examined the logged odds of state transition probabilities as a function of exposed sea urchin density.

### Forest recovery following sea urchin movement

In 2019, we observed a dramatic reduction in counts of sea urchins and an extraordinary recolonisation of a kelp forest to an area that was an expansive sea urchin barren just 2 years prior (2017). Surveys farther inshore (i.e. shallow water) during the recovery year (2019) revealed an abundance of large (>6 cm) sea urchins and a reef devoid of macroalgae. We hypothesised that the observed recovery of kelp to the deep reef area was associated with sea urchin movement to shallow water because the shallow reef was previously dominated by red foliose algae, an alternative sea urchin food source. To test this hypothesis, we examined urchin size structure and density across three depth zones and three survey years. We categorically assigned all the survey sites ( $n = 18$ ) near the recovery area to one of three depth zones: shallow (0–6 m), mid (7–13 m) and deep (14–20 m). Sea urchins were categorically assigned to one of three size classes based on test diameter: small (<30 mm), medium (30–38 mm) and large (>38 mm). These size classes were selected based on the first, second and third quantiles of the entire population size distribution across all three survey years ( $n = 6827$  individuals).

We used a mixed model with a Restricted Maximum Likelihood (REML) to test for differences in mean sea urchin density across three survey years (2017–2019), three depth zones (shallow, mid and deep) and three size classes of sea urchins (small, medium and large). The model was constructed as a full factorial with year, depth zone and size class as fixed effects and site and transect as random effects. We then used a contrast test to examine the hypothesis that the density of large- and medium-sized urchins declined over the period 2018–2019 in the deep zone and simultaneously increased in the shallow zone. The output of the mixed model revealed that the density of sea urchins did not significantly change across the 2017–2018 time period. Therefore, we restricted the subsequent contrast test to the 2018–2019 period.

Finally, we explored changes in the algal assemblage across each depth zone in relation to sea urchin movement. To test for changes in the mean percent cover of foliose red algae, brown algae and encrusting algae, we used an analysis of variance (ANOVA) test on photoquadrats at each survey site with depth zone and algae type as predictors of percent cover. We then used PISCO data on kelp density from an adjacent site located near the recovery area (Pt. Pinos) to examine whether the spatial and temporal kelp recovery at deep reefs was associated with sea urchin movement to shallow water.

## RESULTS

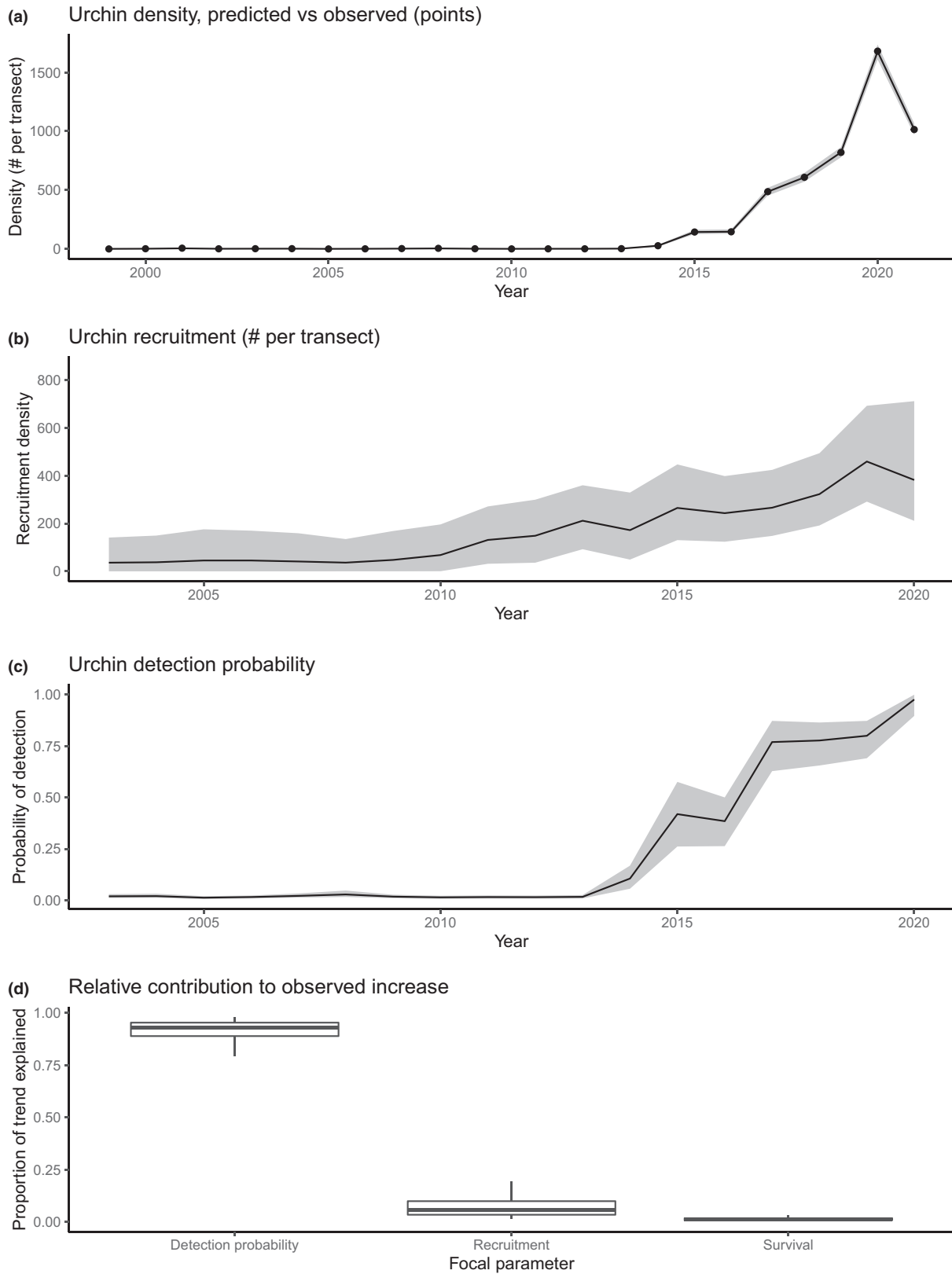
### Sea urchin behavioural shifts at the regional scale

A sharp increase in the density of visually detectible purple sea urchins was initiated in 2014 and continued for at least 6 years before reaching an apparent deceleration (Figure 2a). Prior to 2014, the mean density of visually detectible sea urchins was 3.18 individuals (per 60 m<sup>2</sup> transect). However, the density of visually detectible sea urchins in the 2015–2020 period markedly increased to over 700 individuals (per 60 m<sup>2</sup> transect). Despite the dramatic increase in the density of visually detectible sea urchins, the size frequency distribution of urchins between 2013 and 2014 was similar, although larger urchins (>4 cm) were more frequently detected in 2014 (Figure 3). Moreover, we did not find evidence of an anomalous pulse in urchins at the lower end of the size distribution (<4 cm) in the years prior to 2014.

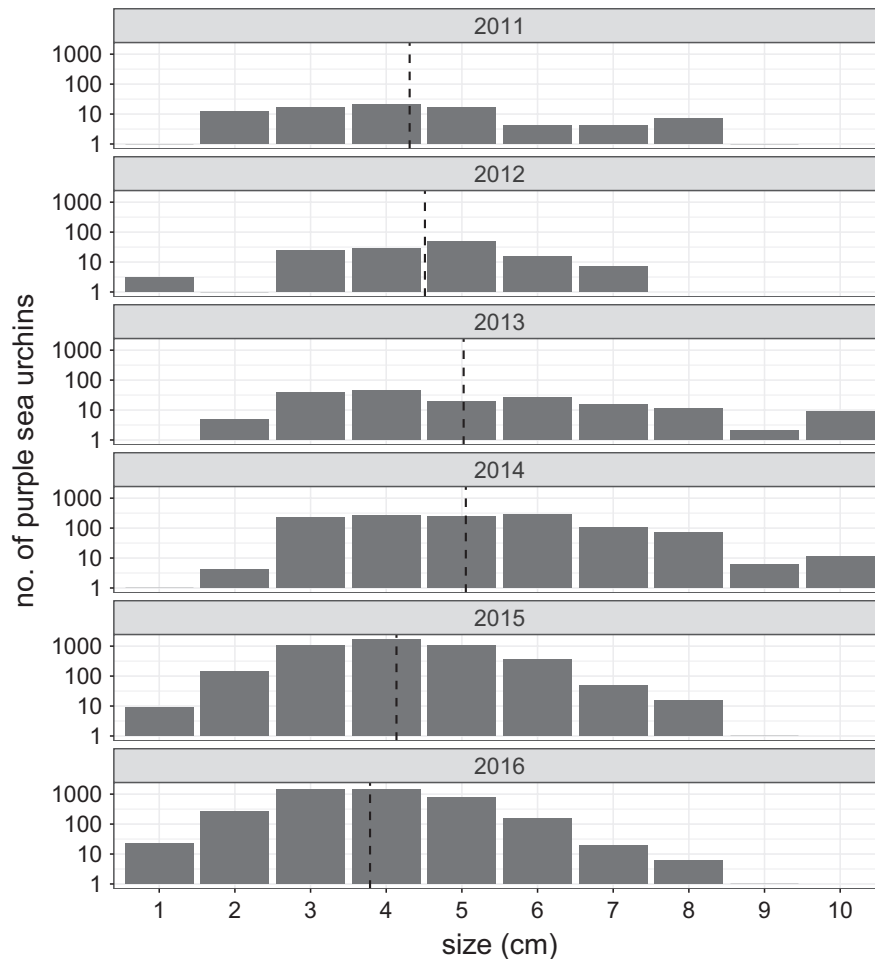
The size-structured population model converged well ( $r$ -hat <1.05 for all fitted parameters) and provided excellent goodness of fit to the survey data, satisfying all posterior predictive checks (Figure S4 and Table T3). The resulting hindcast estimates of density trends and annual size-frequency distributions closely matched field survey estimates (Figure 2a, Figure S7). The model results indicated an increasing rate of recruitment beginning after 2010 (Figure 2b) and an even more dramatic increase in detection probability beginning after 2013 (Figure 2c). The mean detection probability for large urchins increased 37-fold after 2013, as compared to a 5-fold increase in recruitment and no significant change in survival rates (Figure S8). Variation in detection probability alone was able to explain 93% of the observed increase in urchin counts compared to approximately 6% explained by variation in recruitment and 1% explained by variation in survival (Figure 2d). These results suggest that the dramatic increase in counts of purple sea urchins that began in 2014 was explained mostly by a change in the probability that urchins of all size classes were detected, consistent with a behavioural shift (e.g. the emergence of urchins from the refuge).

### Patch-level dynamics

We found support for the hypothesis that patch state transitions are explained by shifts in sea urchin behaviour. The linear discriminant analysis revealed that 113 sites persisted as the same starting and ending state across time steps, 11 forward-shifted from a forest state to barren and 12 reverse-shifted from a barren state to the forest (Figure S9). Model selection for the full logistic regression with behaviour (active, passive) as a predictor of the year-following state showed that the density of actively foraging (i.e. exposed) urchins was the strongest



**FIGURE 2** Trends in purple sea urchins at long-term PISCO subtidal monitoring sites in Monterey Bay, California, USA (Malone et al., 2021). (a) Projections of mean urchin density trends (number per  $60\text{m}^2$  transect) between 1999 and 2021 based on a Bayesian population model, showing mean estimates (solid line), 90% credible interval (grey shaded band) and raw data (solid points). (b) Trends in urchin recruitment density based on the results of a Bayesian population model (solid line shows mean estimates and shaded band shows 90% credible interval). (c) Trends in detection probability for large urchins based on the results of a Bayesian population model (solid line shows mean estimates and shaded band shows 90% credible interval). (d) Boxplot of results from a simulation-based sensitivity analysis, showing the relative contribution of three processes to the observed increase in observed urchin density after 2014: 1) detection probability, 2) annual recruitment rate and 3) annual survival rate



**FIGURE 3** Size frequency distribution of purple sea urchins (*Strongylocentrotus purpuratus*) in Monterey, CA recorded on long-term subtidal monitoring surveys by PISCO (Malone et al., 2021). Each bar depicts the log-number of measured purple sea urchins recorded across 12 discrete size classes (test diameter). Vertical dashed lines indicate the mean size for a given year, weighted by counts for each size class

relative determinant of transition probability ( $R^2 = 0.18$ ,  $p < 0.0001$ ,  $AIC_c = 108$ ,  $\Delta AIC = 10$ ).

An analysis of the logged odds from the logistic regression revealed evidence of a strong discontinuous state shift (Figure 4). The 50% probability transition threshold for a forward shift from a kelp forest to a sea urchin barren was 2.71 exposed urchins/m<sup>2</sup>. However, the 50% probability transition threshold for a reverse shift from a barren to a forest was 0.03 exposed urchins/m<sup>2</sup>.

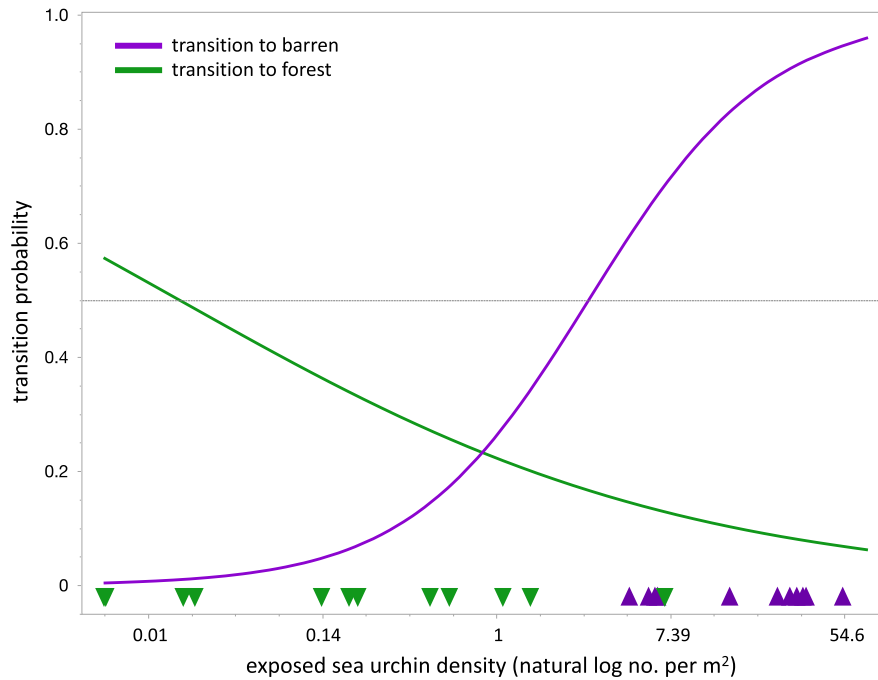
### Forest recovery following sea urchin movement

In 2019, we observed a remarkable recovery of forests at a deep (14–20 m) rocky reef that was an expansive sea urchin barren just 2 years prior (2017). Long-term subtidal monitoring data revealed a rapid decline in kelp density across all depth zones in 2014 that coincided with the onset of sea urchin barrens. Starting in 2018, bull kelp (*Nereocystis luetkeana*) recolonised the deep depth zone, with a sharp uptick in 2019 (Figure 5; Figures S10 and S11).

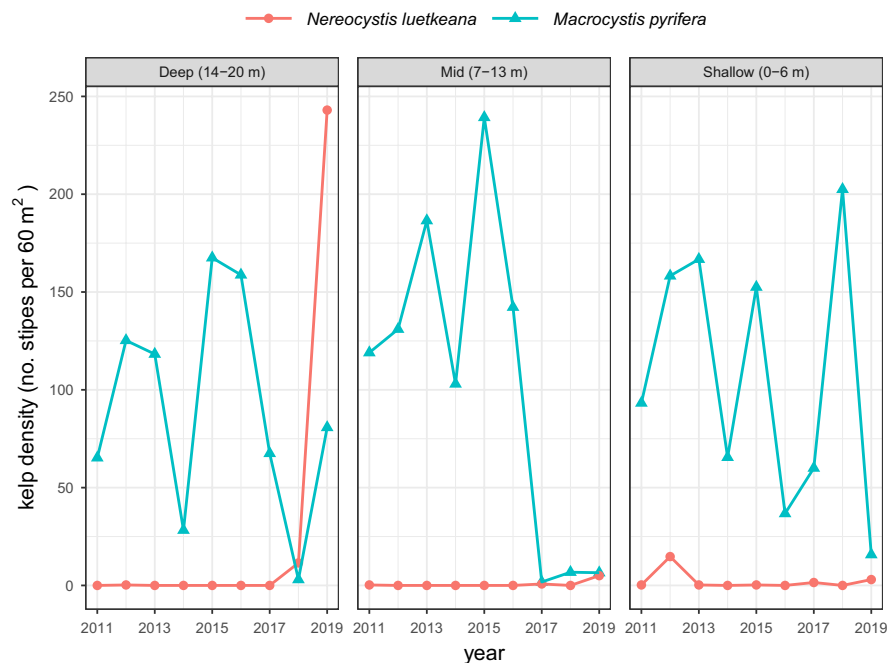
We found that the total density of sea urchins significantly decreased in the deep zone between the 2018 and 2019 sampling seasons, with the most pronounced effects occurring in the large and medium urchin size classes ( $R^2 = 0.53$ ,  $p < 0.0001$ ; Figure 6a). A less dramatic but similar decline in medium and large urchins was observed across the same time step at mid-depths (7–13 m). In the shallow zone, the total mean sea urchin density increased from 1.58 urchins/m<sup>2</sup> ( $\pm 0.34$  SE) to 14.17 urchins/m<sup>2</sup> ( $\pm 1.19$  SE). All size classes of urchins significantly increased in the shallow zone in the 2019 survey year ( $p < 0.0001$ ). The contrast test revealed that the density of large- and medium-sized urchins significantly declined within the deep zone between 2018 and 2019 ( $t$  ratio = 2.77,  $p < 0.005$ ) and increased within the shallow zone during this same time period ( $t$  ratio = -5.69,  $p < 0.0001$ ). Finally, a comparison of slopes between the deep and shallow zones across the 2018 and 2019 periods revealed that they were significantly different (DenDF = 2765,  $F = 20.16$ ,  $p < 0.0001$ ).

Results from analyses on the percent cover of foliose red algae, brown algae and encrusting algae further support





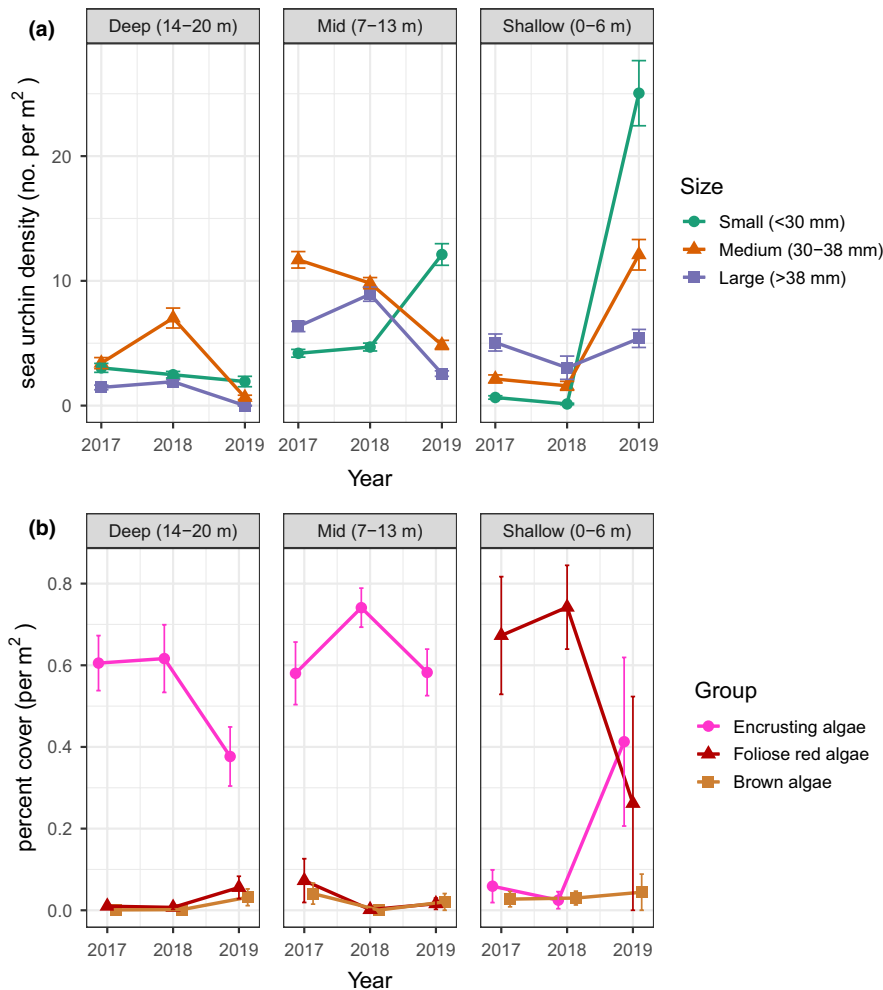
**FIGURE 4** Transition probabilities depicting simulated logged odds for each starting state based on the log-transformed density of exposed sea urchins. The purple line depicts the probability of a forest patch transitioning to a sea urchin barren in the following year based on the starting density of exposed sea urchins, and the green line depicts the probability of a barren becoming a forest in the following year. Also included are triangles that depict the final density (no. per  $m^2$ ) of exposed sea urchins for patches that transitioned (green triangles are patches that became forests, purple are patches that became barren). The dashed horizontal line indicates the 50% probability transition threshold



**FIGURE 5** Kelp dynamics at Pt. Pinos, California, USA. Each line depicts the annual mean density (per  $60 m^2$  transect) of giant kelp (*Macrocystis pyrifera*, blue) and bull kelp (*Nereocystis luetkeana*, orange) across three depth zones recorded by PISCO (Malone et al., 2021)

the hypothesis of mass sea urchin movement to shallow water. Starting in 2019, the cover of encrusting coralline algae significantly decreased in the deep zone, along with a simultaneous increase in the cover of foliose red and

brown algae ( $R^2 = 0.79$ ,  $DF = 2$ ,  $p < 0.0001$ ; Figure 6b). In the shallow zone, the cover of foliose red algae significantly decreased, with a pronounced uptick in the cover of encrusting coralline algae ( $R^2 = 0.33$ ,  $DF = 2$ ,  $p < 0.0001$ ).



**FIGURE 6** Urchin movement dynamics and algae percent cover across three depth zones. Panel (a) depicts the mean density of small (<30 mm), medium (30–38 mm), and large (>38 mm) purple sea urchins. Panel (b) depicts the mean cover of foliose red algae (red), encrusting red and coralline algae (pink) and brown algae (brown). Error bars are included as 95% confidence intervals

## DISCUSSION

This study demonstrates the important role of grazer behaviour in facilitating patch-state transition dynamics. The kelp forest-urchin barrens mosaic that developed following the extirpation of *Pycnopodia* and the marine heatwave revealed how grazer behaviour shapes alternations between kelp-dominated and urchin-dominated states. These findings suggest that the initial 2014 sea urchin outbreak along southern Monterey Bay, California was primarily driven by the emergence of adult sea urchins from refuge, not by a demographic response (i.e. recruitment). Behaviourally driven alternations among patch states across the mosaic further demonstrate the role of grazer behaviour in facilitating transition dynamics.

In many systems, behaviour is a primary mechanism for the organisation of ecological communities (Karatayev et al., 2021; Lima & Zollner, 1996; Werner & Peacor, 2003). However, behavioural-driven community patterning often results from demographic (i.e.

recruitment) or density-dependent responses of predators and their prey (Levin, 1976). Our study supports how multiple biotic (e.g. recruitment, loss of key predators) and environmental (e.g. marine heatwaves, grazer metabolic responses to warming events) perturbations may interact to influence behavioural switching that can facilitate persistent patterning of community states. The initial sea urchin outbreak observed in this region in 2014 is likely reflective of a shift in grazing modality (from passive to active grazing), potentially in response to several coinciding factors such as reduced food availability, increased metabolic demands from the warming event (e.g. Rasher et al. 2020), recruitment leading to adult behavioural switching and from a reduction in the abundance of a benthic mesopredator (Burt et al., 2018; Cowen, 1983; Harrold & Reed, 1985).

While we did not find strong evidence of a demographic response coinciding with the 2014 sea urchin outbreak, recruitment facilitation is a known driver of alternative state dynamics (Baskett & Salomon, 2010; Karatayev et al., 2020). Sea urchin recruitment dynamics

are often episodic, with considerable geographic variation (Ebert & Russell, 1988; Okamoto et al., 2020; Pearse & Hines, 1987). Following the initial sea urchin behavioural shift in 2014, it is possible that the formation of barren patches enhanced sea urchin recruitment to barrens within the mosaic. Another alternative hypothesis is that increased sea urchin recruitment may have led to the observed behavioural response in adults, especially after 2014. Additionally, recruitment may have occurred prior to 2012 in this system or with variable timing and magnitude at other locations along the northeastern Pacific Ocean (Okamoto et al., 2020; Rogers-Bennett & Catton, 2019).

Long-term monitoring observations along the central coast of California, USA indicated that the 2014 sea urchin outbreak continued for at least 6 years and was potentially reinforced by recruitment after 2014. During this same period, canopy-forming kelps to the north and south of the study region experienced unprecedented declines resulting from the marine heat-wave and even more expansive outbreaks of purple sea urchins (Arafah-Dalmau et al., 2019; Beas-Luna et al., 2020; McPherson et al., 2021; Rogers-Bennett & Catton, 2019). One explanation for the persistence of remnant kelp patches in this system (as opposed to adjacent neighbouring areas) is the presence of trophically redundant predators. The urchin predator guild along the west coast of North America is comprised of six key species: sea otters (*Enhydra lutris nereis*), lobsters (*Panulirus interruptus*), sheephead (*Semicossyphus pulcher*), sunflower sea stars (*Pycnopodia helioanthoides*), rock crab (*Cancer* spp.) and wolf eels (*Anarrhichthys ocellatus*; Scheibling & Hamm, 1991; Eisaguirre et al., 2020). The abundance of these species varies geographically along the west coast. In northern California, where rock crab and wolf eels are the only alternative predators of urchins, forests were reduced by over 95% with the loss of *Pycnopodia* (McPherson et al., 2021). However, forests in southern California that have a suite of urchin predators (e.g. lobster, sheephead, rock crab) experienced an apparent buffer from kelp decline following the demise of *Pycnopodia* (Eisaguirre et al., 2020). Finally, on the central coast of California, remnant patches of kelp forests were indirectly maintained by sea otters that target energetically profitable sea urchins in patches of forest (Smith et al., 2021). This spatially explicit foraging by sea otters is likely the mechanism responsible for the persistence of kelp patches within the mosaic.

In this study, switching among patch states within the mosaic was explicable in part by changes in the density of exposed (i.e. active foraging) sea urchins. Behavioural switching within the mosaic across such a short temporal duration may be driven by spatial variability in drift kelp. High levels of drift kelp have been shown to facilitate reef-scale behavioural feedback in California, Chile and New Zealand (Karatayev

et al., 2021; Kriegisch et al., 2019; Ling et al., 2019; Vásquez & Buschmann, 1997). We also found evidence of strong discontinuous state shift thresholds, with at least two discontinuous thresholds required to facilitate switching among patch states. A number of studies have suggested a critical threshold of a forcing variable that drives state transitions to less productive configurations (Casini et al., 2009; Petraitis & Dudgeon, 2004). The strong forward- and reverse-shift thresholds identified in this study provide an empirical demonstration of this phenomenon.

Sea urchin movement from deep to shallow water may explain the isolated recovery of kelp forest patches in deep water. The dramatic reduction in medium- and large-sized urchins at deep reefs, simultaneous increase of those size classes inshore and the pronounced reduction of foliose red macroalgae in shallow water all indicate that sea urchin movement is one possible explanation for the observed changes in the cover of macroalgae. Although other studies have documented sea urchin migrations between depth zones (Ling et al., 2016; Vadas et al., 1986), an alternative explanation in this system is that sea urchins occupying the deep reefs switched to a passive-grazing modality and those in the shallow zone emerged from the refuge. However, because there was not a reduction of macroalgae in the shallow zone prior to the increase in the density of medium- and large-sized urchins, the movement hypothesis (as opposed to behavioural switching) remains the most parsimonious explanation for observed recovery dynamics.

At the locations where kelp recovery was observed, it is important to note the kelp species that repatriated the once barren grounds was the bull kelp (*Nereocystis luetkeana*, a predominately annual species), not the giant kelp (*Macrocystis pyrifera*, a perennial species). Prior to the 2014 sea urchin outbreak, kelp forests along the Monterey Peninsula were dominated by the giant kelp (Foster & Schiel, 1985; Graham et al., 1997). It is well established that shading by giant kelp limits algal recruitment and the growth of other non-calcareous species (Kennelly, 1989; Reed & Foster, 1984). The removal of long-standing giant kelp forests by purple sea urchin grazing may have released *Nereocystis* from light limitation, thereby enabling the rapid recolonisation and growth of *Nereocystis* following sea urchin movement inshore to shallow water.

The results presented in this study highlight the role of behaviorally mediated effects in structuring ecological communities. One of the most unusual aspects of this system is the ability of sea urchins to persist in low-resource environments for extended periods of time (Ebert, 1967; Ebert, 1982; Smith & Garcia, 2021), which may contribute to the longevity of the alternative barrens state of the ecosystem. Therefore, the behaviour of grazers, especially ecosystem engineers, is fundamental to community and ecosystem dynamics.

## AUTHORS CONTRIBUTION

JGS conceived the study, performed the analyses and wrote the first draft of the manuscript. MTT developed the population state dynamics model, contributed to manuscript and model revisions and provided substantial conceptual input.

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## DATA AVAILABILITY STATEMENT

Data and source code are available on GitHub (<https://github.com/joshsmith/PatchDynamics>).

## PEER REVIEW

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## ORCID

Joshua G. Smith  <https://orcid.org/0000-0003-4633-4519>  
M. Tim Tinker  <https://orcid.org/0000-0002-3314-839X>

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### Supporting Information

Additional supporting information may be found in the online version of the article at the publisher's website.

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## REVIEW

# Building mountain biodiversity: Geological and evolutionary processes

Carsten Rahbek<sup>1,2,3,\*†</sup>, Michael K. Borregaard<sup>1†</sup>, Alexandre Antonelli<sup>4,5</sup>, Robert K. Colwell<sup>1,6,7</sup>, Ben G. Holt<sup>1</sup>, David Nogues-Bravo<sup>1</sup>, Christian M. Ø. Rasmussen<sup>1,8</sup>, Katherine Richardson<sup>1</sup>, Minik T. Rosing<sup>9</sup>, Robert J. Whittaker<sup>1,10</sup>, Jon Fjeldså<sup>1,7</sup>

Mountain regions are unusually biodiverse, with rich aggregations of small-ranged species that form centers of endemism. Mountains play an array of roles for Earth's biodiversity and affect neighboring lowlands through biotic interchange, changes in regional climate, and nutrient runoff. The high biodiversity of certain mountains reflects the interplay of multiple evolutionary mechanisms: enhanced speciation rates with distinct opportunities for coexistence and persistence of lineages, shaped by long-term climatic changes interacting with topographically dynamic landscapes. High diversity in most tropical mountains is tightly linked to bedrock geology—notably, areas comprising mafic and ultramafic lithologies, rock types rich in magnesium and poor in phosphate that present special requirements for plant physiology. Mountain biodiversity bears the signature of deep-time evolutionary and ecological processes, a history well worth preserving.

Mountains are topographically complex regions formed by the interplay of tectonic and volcanic processes. They are intrinsically unstable systems, undergoing substantial changes in response to tectonic, erosional, and climatic processes over geologically short time scales. The interaction of mountain substrates, life forms, and climate systems—at a range of spatial scales—establishes diverse and distinct montane environments (1–4). These environments are transient, and their ongoing changes drive the splitting and subsequent isolation of species ranges, evolutionary adaptation to changing conditions, and consequently, population differentiation. These biological processes create a shifting balance between speciation and extinction, in which mountains may act as “cradles” (areas of especially rapid species origination), “museums” (areas of especially long-term persistence of species), and “graves” (areas with especially high rates of extinction) for biodiversity (1, 5). The high levels of richness and endemism of species on most mountains thus reflect enhanced speciation, coexistence, and persistence of evolutionary lineages with distinct evolutionary trajectories.

Mountain regions, especially in the tropics, are home to aggregations of small-ranged species (6) that form highly diverse centers of endemism. These aggregations cannot be predicted from underlying global patterns of species richness (7) or by models that are based purely on contemporary ecological conditions (3). One possible explanation is that statistical models have not adequately captured the high spatial heterogeneity of ecological and environmental variables characteristic of mountains (3). However, current mountain diversity may also bear the signatures of deep-time evolutionary and ecological processes, driven by changing climate over topographically complex landscapes and by biotic interchange with neighboring areas (1, 5, 8). The fluctuating dynamics of mountain speciation, evolutionary adaptation, dispersal, persistence, and extinction may ultimately explain diversity patterns across entire continents.

Geological dynamics are increasingly recognized as a key driver of these evolutionary processes, influencing the buildup (and sometimes decline) of mountain diversity (1, 2, 4). The fossil record allows robust analyses of how species diversification in mountain landscapes has been affected by the break-up and merging of lithospheric plates, in the context of plate tectonic processes (9, 10), and by changes in global temperature (11). Linking biogeographical dynamics to detailed reconstructions of mountain formation has become increasingly feasible through such analyses (10). Here, we discuss how evolutionary processes associated with climate history, orogenic processes, and the geological composition of mountain regions shape large-scale geographical patterns of species diversity.

## Key roles of mountains for biodiversity

Over long periods of time, topographic, geological, and geophysical conditions modify the rates

and properties of four key processes that determine the distribution and diversity of life on Earth: speciation, dispersal, persistence, and extinction (Table 1). The emergence of the Andes, for example, influenced plant diversification and evolution in South America in at least four different ways: (i) by creating a region of novel, high-elevation habitats for species; (ii) as a dispersal barrier to lowland organisms, splitting populations east and west of the mountain range, as well as internally in valleys and peaks; (iii) as a north-south corridor for species dispersal; and (iv) as a modifier of environmental, hydrological, and mineralogical conditions in the rest of the continent, through montane effects on the climate system and as a source of mineral components released by continued erosion and weathering (12, 13).

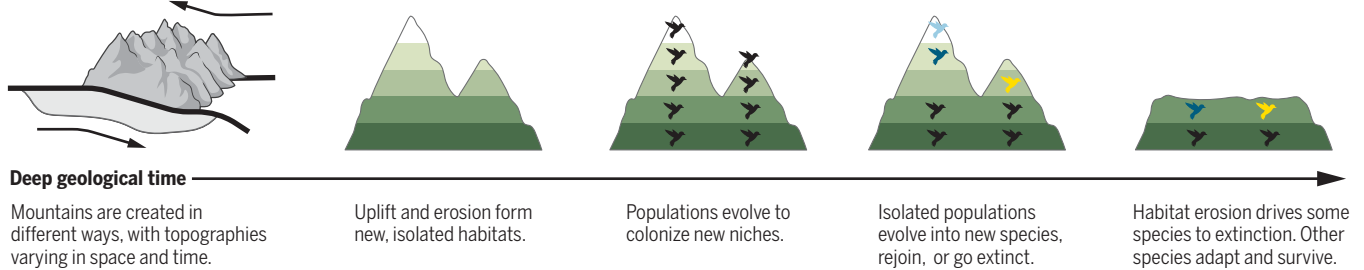
The impact of mountain regions on biodiversity extends far beyond their topographical limits, often affecting entire continental biotas. For example, although the Andes region is in itself the most biodiverse region on Earth, Andean orogeny is also considered a key driver for the buildup of biodiversity across all of South America (13). Over roughly the past 10 million years, Andean orogeny has changed the regional topography repeatedly, forcing the Amazon drainage basin to change its course. These changes altered gene flow across the Amazonian lowlands, affecting both terrestrial and aquatic biogeography (14). Mountain regions may also play a role as sources of new evolutionary lineages that later colonize lowland regions. Phylogenetic and biogeographical reconstructions reveal an Andean origin for many Amazonian species, including plants (12), amphibians (15), and tanagers (16).

The influence of specific mountain ranges on the biodiversity of broader regions and entire continents depends on their geographical location, spatial orientation, local biotic context, and history (2). Thus, the European Alps, oriented east-west, have been recognized as refugia for cold-adapted species but provide insufficient habitat connectivity to enable the persistence of many late-Neogene lineages in Northwestern Europe through the Pleistocene (17). By contrast, the north-south-oriented Rocky Mountains have facilitated latitudinal range adjustments, providing dispersal corridors during fluctuating climates and boosting the persistence of North American Neogene populations and species through Pleistocene glacial-interglacial climate cycles (18). These processes are often cited to explain why the tree flora of Western Europe is so depauperate in comparison with the tree flora of North America (18).

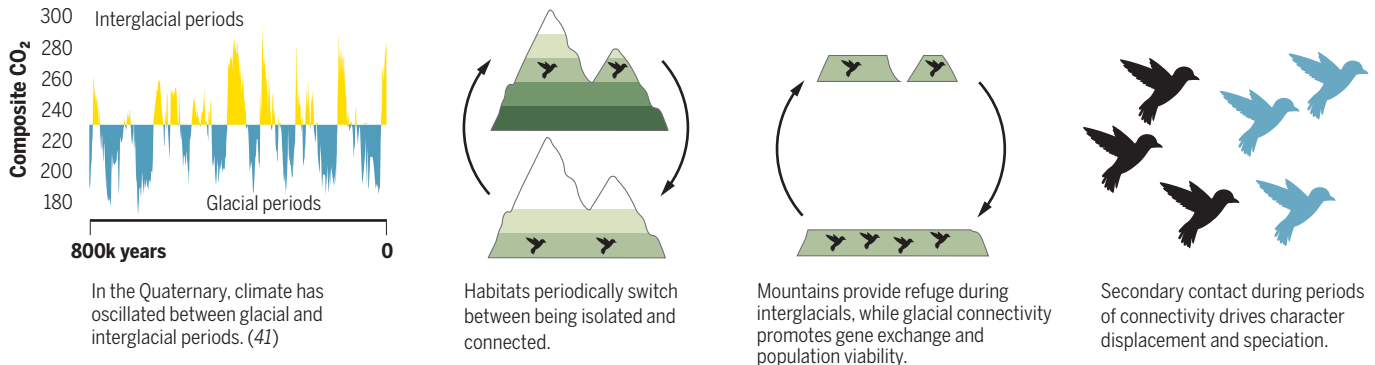
The influence of mountains likely differs among taxonomic groups. Speciation in plants, for example, often reflects adaptations to particular soil geochemistry and mineralogy (19). In birds, speciation may be more susceptible to the breakup of species ranges that follow narrow elevational habitat bands. These include shifts in the tree line and the cloud forest belt (20) and the fragmentation of geographic ranges by major rivers (21). For invertebrates, many speciation events are

<sup>1</sup>Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Denmark. <sup>2</sup>Department of Life Sciences, Imperial College London, Ascot SL5 7PY, UK. <sup>3</sup>Danish Institute for Advanced Study, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark. <sup>4</sup>Royal Botanic Gardens, Kew, Surrey TW9 3AE, UK. <sup>5</sup>Gothenburg Global Biodiversity Centre, SE-41319 Göteborg, Sweden. <sup>6</sup>Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA. <sup>7</sup>University of Colorado Museum of Natural History, Boulder, CO 80309, USA. <sup>8</sup>Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark. <sup>9</sup>Section for GeoBiology, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark. <sup>10</sup>School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK. \*Corresponding author. Email: crahbek@snn.ku.dk †These authors contributed equally to this work.

## A Orogeny—Creating new species over millions of years



## B Dynamic changes in connectivity—Speciation driven by mountain climate cycling



**Fig. 1. Schematic view of two temporal scales of buildup of mountain diversity. (A)** Mountain ranges are tectonically dynamic over millions of years, leading to isolated changing environments and the long-term adaptation of species colonizing these new habitats. **(B)** Climatic dynamics in the Quaternary, induced by Milankovitch orbital cycles, caused habitats and climatic zones to move up and down mountain slopes, repeatedly, on the scale of tens of thousands to hundreds of thousands of years. These movements led to rapid, repeated dynamics of range splitting and secondary contact, stimulating diversification. [Graph at left is based on publicly available data (41).]

likely to follow plant specialization linked to the production of specific metabolites.

### Evolutionary processes in mountains

Mountains are hotbeds of speciation, influenced by geological and climatic dynamics over deep time. Mountains can form during both compression and stretching of the lithosphere. Orogeny—mountain building—typically includes tectonic stacking of lithosphere domains of diverse age, origin, and composition, including upducted ocean floor, emplacement of intrusive magmatic bodies, and building of surface volcanic structures. Mountains are thus lithologically and topographically heterogeneous regions. Evolutionary radiations of species are often associated with phases of active uplift, suggesting that orogenic processes play a role in driving diversification (Fig. 1A) (14, 22, 23), principally through the recurrent formation, connectivity, and disappearance of habitats within mountain ranges (Fig. 1A) (24). Orogenic dynamics, including surface uplift and formation of intermontane basins and subsequent erosion, create shifts in hydrological catchments, river flows, and nutrient fluxes. These processes change soil composition and nutrient levels, driving adaptation of plants and their associated biota in new habitat types. Mountain formation also affects local climate,

creating zones of rain shadow or persistent mist, with a strong filtering effect on species communities (2).

During the past ~2.6 million years, the climatic cyclicity of the Quaternary has impelled dynamic shifts in habitat connectivity that stimulated speciation in certain groups (Fig. 1B) (25). These changes are linked to the Milankovitch eccentricity cycle, with a periodicity of around 100,000 years, possibly amplified by the ~41,000-year obliquity cycle, and are further thought to instigate cyclic, climate-driven habitat changes that drive temporally rapid “species pumps” (10, 25, 26). Vegetation belts moved upslope during warm and wet interglacials, leading to the fragmentation of populations and genetic divergence. As temperatures dropped again in glacial episodes, vegetation belts moved downslope, forcing secondary contact of populations, leading to founder effects, disruptive selection, and character displacement, thus creating the conditions classically associated with allopatric speciation. In a process-based simulation model of range dynamics in South America, Rangel *et al.* recently found support for these predictions, with the Andes acting as an episodic species pump (Fig. 1B) (5).

At large spatial and temporal scales, these processes can yield very different distributions of species, some that descended from ancient,

isolated lineages and some that originated from recent radiations. The relative contribution of these two groups to mountain diversity varies greatly among mountain regions [compare Fig. 2 with (3), figure 3]. Badgley *et al.* defined specific, testable predictions from three (nonexclusive) models for the occurrence of radiations in topographically complex landscapes: (i) Active tectonic dynamics drive speciation, (ii) speciation is constantly elevated in the habitat mosaic of topographically complex areas, and (iii) climate-driven immigration stimulates speciation (4). In an empirical study of North American rodents, Badgley and colleagues found some support for the first and third scenarios (4). In a recent global analysis, Antonelli *et al.* also found a substantial effect of mountain relief on species diversity, although with relatively weak effects of erosion and erosive potential, which are otherwise formative influences within geologically dynamic landscapes (2).

### Mountains—Cradles, museums, or graves of diversity?

Stebbins (27) famously asked whether species diversity in the tropics is so high because the tropics are cradles (areas of especially rapid species origination) or museums (areas of especially long-term persistence of species). Other

metaphors have since been added (Table 1), including the notion of graves to describe geographical areas with especially high rates of extinction. Identification of graves from contemporary distribution data or fossils remains elusive. However, their existence, location, and timing have been predicted with process-based simulation models (28) of geographical range dynamics through time, driven by simulated paleoclimates (5).

For the most diverse tropical mountains, it appears that the answer to Stebbins's question is that mountains are both cradles and museums (Fig. 2C) (29). To exemplify, the Andes not

only are home to several recently diversified species clusters with high phylogenetic relatedness but also host many old, relictual lineages aggregated in centers of endemism (30). The combination of both cradle and museum effects appears crucial to the emergence of the Andes as the most diverse region on Earth (3).

Whereas the Andes have high numbers of both early divergent and recently derived species, the mountain regions of Southeast Asia are primarily occupied by species that are recently derived (Fig. 2). A plausible explanation for these regionally distinct patterns is that tropical mountain ranges with very high peaks and more rugged

terrain, such as the Andes and Southeast Asia, are home to a high-elevation biota characterized by a small number of lineages adapted to colder environments. These few lineages may become regionally very species-rich as a product of rapid, local diversification (31). In the Andes, this process may have occurred more repeatedly than in Southeast Asia. By contrast, the Afrotropical regions and the Atlantic Rainforest mountain region of South America both show a greater predominance of early divergent species.

In a simulation of temporal range dynamics of the South American biota, cradles derived from Andean founders (each simulation began with one initial "seed" species) were found to be concentrated along the Andean slopes, whereas graves tended to be at lower elevations in the upper Amazon Basin (5). By contrast, biotas derived from Atlantic Forest founders had a much higher spatial coincidence of cradles and graves. These results align with the view that topographic complexity and elevational climate gradients promote range fragmentation and act as cradles, while at the same time acting as museums by providing climatic refugia from extinction (5, 26, 32). The simulations also revealed that the spatial positions of cradles, museums, and graves can be dynamic, changing shape, size, and intensity over time and in response to Quaternary climate cycles (5). These temporal and spatial dynamics imply that inferring cradles or museums on the basis of the current distributions of extant young and old lineages may be misleading.

### Geological heterogeneity and biodiversity

The potential importance of mountain geology, including the mineralogical composition of substrates, has been highlighted in recent work (1, 2, 4). Mountain substrates generally differ substantially from those of surrounding lowland basins, which are frequently dominated by eroded materials derived from the mountains and deposited in valleys and plains. Mineral composition and nutrient levels in the soil affect plant physiology, vegetation composition, primary productivity, and consequently, species diversity. In addition, mountain regions with a high level of geological heterogeneity are likely to support higher levels of species spatial turnover and local endemic forms, particularly among plants. However, empirical studies that establish a relationship between diversity of edaphic conditions and plant species diversity are scarce, and little is known about how edaphic heterogeneity affects diversity at higher trophic levels.

In a recent global analysis, which also confirmed the classic correlation of species diversity with topographic relief and climate (3, 33, 34), Antonelli and co-workers found correlations of species richness of mammals, birds, and amphibians with both long-term and short-term erosion rates and a measure of soil diversity (2). Although the association was generally weaker than the correlation of richness with climatic variables, soil heterogeneity was consistently a significant predictor of richness across multiple

**Table 1. Proposed biogeographical roles of mountains, the key processes involved, their underlying mechanisms, and examples of outstanding research questions.**

Role of mountains	Process	Mechanism	Exemplar questions
Cradles	Speciation and diversification	Fragmentation of species ranges, with potential for local adaptation of populations	What drives adaptive diversification in mountains, and how important is nonadaptive speciation?
Innovation hubs	Adaptive radiation	Adaptive response of isolated populations in a heterogeneous environment to local selection	Do higher environmental ultraviolet levels directly affect mutation rates? Do localized, distinctive soils generate speciation cascades?
Elevators	Dispersal (passive)	Passive movement of species and their substrates from lowlands caused by surface uplift	How can we differentiate between passively uplifted species and those actively dispersed?
Corridors	Dispersal (enhanced)	Continuous linkage of similar highland habitats	What are the relative contributions of local recruitment versus long-distance dispersal to high-elevation biotas?
Barriers	Dispersal (blocked)	Vicariance of lowland species, preventing further gene exchange	How can we test this hypothesis, given uncertainties in paleoclimatic models, molecular data, and geological reconstructions?
Reservoirs	Maintenance	Persistence of species during climate change by tracking their climate niche through elevational range shifts	How do species persist on mountains with limited possibility for elevational migration or discordant shifts in temperature and precipitation?
Refugia	Maintenance	Mountains acting as sources to restock lowlands after episodes of climate-driven extinction	How representative is the Last Glacial Maximum for the role of mountains as refugia in the context of previous glaciations?
Museums	Maintenance	Collapse of once-larger ranges, leaving remnant populations in favorable mountain microclimates	How important is climatic and topographic complexity for the persistence of lineages?
Sinks	Extinction	Local extirpation due to patchy habitat availability	How does the role of sinks vary with latitude?
Graves	Extinction	The failure of species to disperse to suitable climates or adapt, under changing conditions	How important will mountaintop extinctions be, compared with human-induced landscape changes?



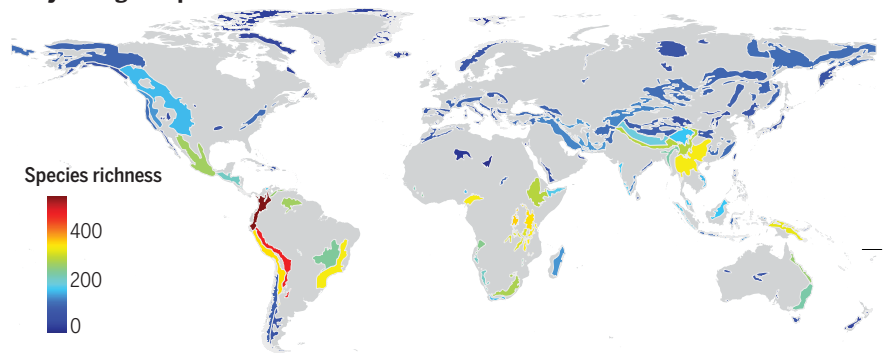
biogeographical regions of the world. Antonelli and co-workers suggested that soil heterogeneity underlies fine-scale habitat turnover, creating new habitats and ecological opportunities, increasing local and regional species richness. In Fig. 3, we further explore the relationship between species diversity and bedrock heterogeneity, as measured by the number of major categories of bedrock that are represented within each mountain region.

Geological heterogeneity, simplified in this way, does not explain much of the variation in total species richness and fails to account for the high richness of small-ranged species that is characteristic of mountains at low latitudes [compare Fig. 3A with (3), figure 3]. This disconnect may imply that the way rock classes translate into ecologically relevant soil properties is substantially more complex than captured by our simple classification. An ecologically relevant special case is the presence or absence of mafic and ultramafic rocks (Fig. 3C). Soils originating from ultramafic rocks have a well-described effect on plant adaptations and diversity. Their unusual geochemistry, with high magnesium content and low availability of phosphorus (35), demands specific adaptations and slows growth rates for plants. The vegetation of serpentine soils, which form on ultramafic bedrock, is highly specialized and generally woody, with high levels of phenols and lignin in leaves, driving secondary effects on the cycling of nutrients in the decomposition of leaf litter. Serpentine soils pose strong selective filters for plants, excluding many groups but fostering radiations of clades that tolerate these soils (36). Ultimately, habitat heterogeneity, patchiness, and specialized dietary adaptations of herbivores may impel speciation cascades in these habitats across all major groups of organisms, including vertebrates.

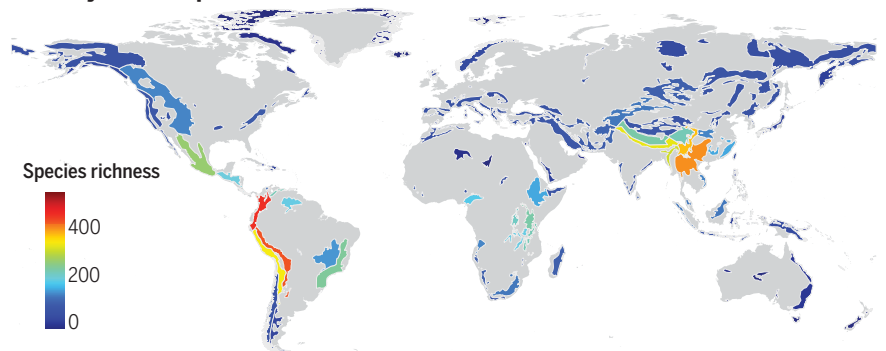
Mapping the global occurrence of larger, contiguous mafic and ultramafic rock domains in mountain regions (Fig. 3B) reveals that all hyperdiverse mountain regions are rich in such rocks. Intercalated mafic and ultramafic rock domains often form part of ophiolites, slivers of oceanic lithosphere upducted and emplaced within continental orogens during plate collision. Emplacement of ophiolites is thus an integral part of the orogenic processes that form cordilleran mountain chains. Ultramafic and mafic rock, mostly associated with ophiolites, underlie >5% of the dark red area in Fig. 3B.

Almost all the most biologically diverse mountain regions have three features in common: high rock diversity, presence of upducted oceanic lithosphere, and a geographical location in the humid tropics (Fig. 3C). By contrast, mountains with low rock diversity and without ultramafic components, even in the mesic tropics, tend to be relatively species-poor. Mountain regions without oceanic lithosphere components show little relationship between biodiversity and rock diversity, regardless of climatic zone. Understanding the geochemical contrast between continental and oceanic lithosphere components may thus be key to understanding how bedrock geology

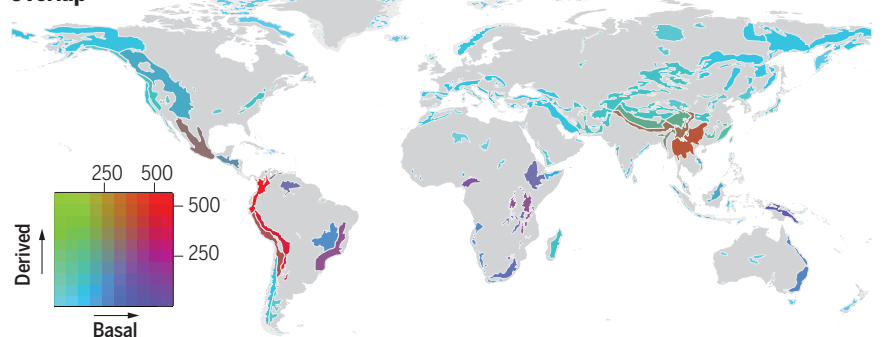
### A Early divergent species



### B Recently derived species



### C Overlap



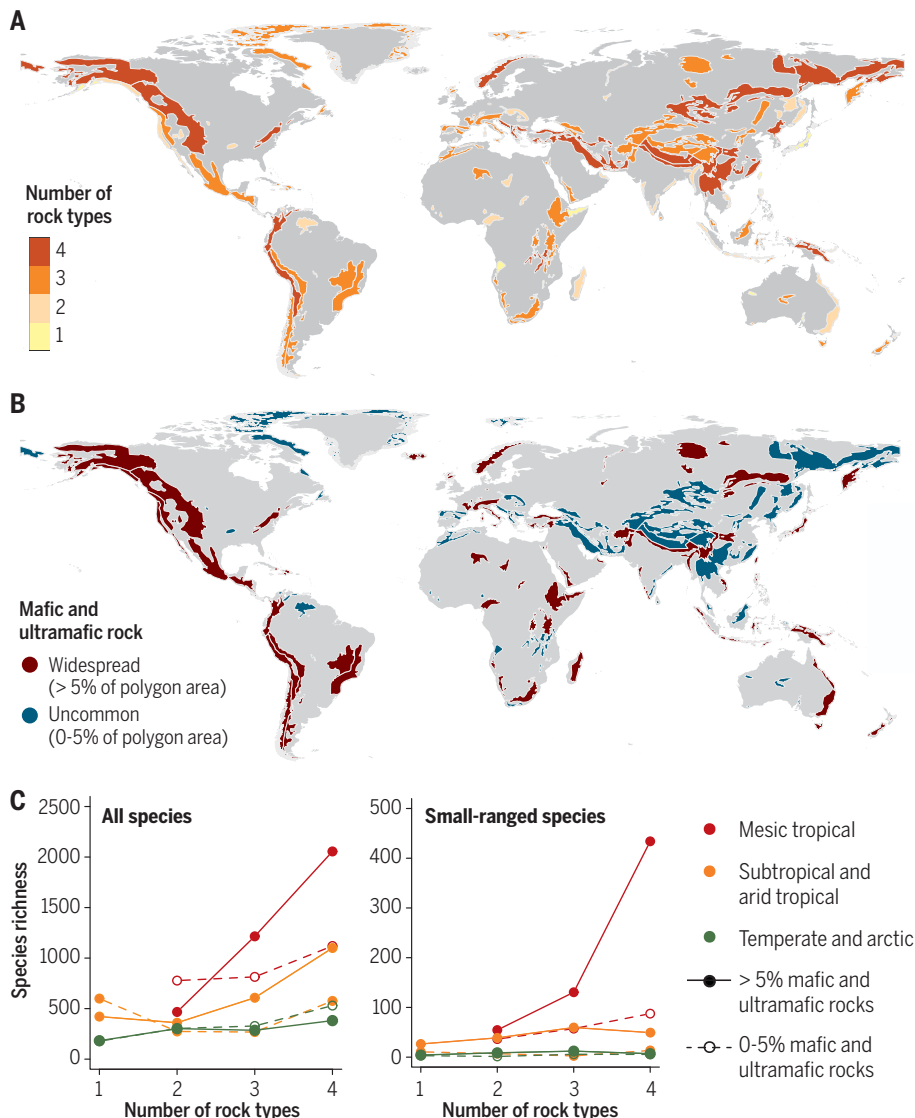
**Fig. 2. Global richness pattern of early divergent and recently derived species in mountain regions.**

(A) The number of early divergent birds, mammals, and amphibians, defined as the 25% of species that are separated from the crown node of their class in the molecular phylogeny by the smallest, ranked node distance. (B) The number of recently derived species among the 25% with the largest, ranked root distance from the crown node. (C) The overlap of early divergent and recently derived species reveals which mountain regions represent museums (purple), cradles (green), or both (red). Light blue areas have low richness of both groups. Distribution and phylogeny data are from Holt *et al.* (42), and mountain regions are as defined in Rahbek *et al.* (3). The classification into early divergent or recently derived was done independently for each class, and values for all three classes were added to give the depicted total.

might influence the production and maintenance of species richness.

The high turnover of distinct habitat patches created on geologically heterogeneous surfaces, even within the same local climate, might contribute substantially to the process of population-splitting and differentiation that characterizes mountain speciation dynamics. Plant characteristics on soils derived from emplaced ultramafic rocks may also pose challenges for herbivorous

animals. Soil geochemistry affects plant metabolism and may increase the production of secondary metabolites, with plants on these soils investing heavily in chemical and physical defenses against herbivores. Such adaptive challenges facing the plant-dependent fauna may stimulate a higher rate of adaptive divergence among consumers during phases of population isolation and thus precipitate locally extremely high rates of diversification, as seen in nectarivores



**Fig. 3. Mountain geology and vertebrate diversity.** (A) Geological diversity, quantified by categorizing rocks on the basis of mineral composition and depositional setting, and counting the number of categories occupying at least 5% of the area of each mountain region. Categories are (i) siliciclastic and (ii) carbonate sedimentary rocks, (iii) metamorphic rocks, and (iv) felsic and (v) mafic igneous rocks. The map shows counts, not categories. (B) The occurrence of mafic and ultramafic rocks, most commonly derived from upducted oceanic lithosphere in mountain regions. Soils formed on these rocks have distinct geochemical properties that require specialized plant metabolism. (C) Richness of all species and of the 25% of species with the smallest ranges, for mountain regions, as a function of geological diversity, climate band, and the widespread occurrence of mafic and ultramafic rocks. Points show the mean value for each category. The richest mountain regions of the world are geologically diverse mountains in the tropics with ultramafic rocks. Mountain regions follow Rahbek *et al.* (3), and the geological data were compiled from sources at <http://onegeology.com>.

(such as hummingbirds) and frugivores (such as New World sparrows and tanagers).

### Concluding perspective

The idea that geology and biology are intertwined runs as a consistent undertone in von Humboldt's *Cosmos*, expressed as his "unity of nature" (37). Later, in 1880, Wallace inferred the recurrence of glaciations in Earth's history from the distribution of related animal species

on islands in the Indo-Pacific (38). Although much research has been stimulated by these early works, the lack of data and robust analytical frameworks has long hampered efforts to fully incorporate biological and geological processes into rigorous statistical models for mountain species diversity and evolution (2).

New methods in geomorphology—including stable isotope altimetry, thermochronology, and advances in digital multispectral imaging (39)—

are paving the way for accurate reconstructions of geological dynamics, thus creating a strong foundation for testing evolutionary theories on the origin and maintenance of mountain diversity over time. Combined with genomic sequencing, these approaches may allow inference of the timing, and perhaps even the location (by using environmental ancient DNA), of changes in effective population sizes and genetic bottlenecks. The next generation of geologically and evolutionarily explicit models may, in this way, radically change our understanding of biotic evolution and resolve the historically contentious debate over the extent to which ecological and evolutionary processes, historical contingency, or simply stochasticity and time shape the diversity and distribution of life on Earth.

The idea that heterogeneity in geological substrate properties may directly affect evolution is still based primarily on circumstantial evidence, supported by statistical patterns with weak or mixed correlations with diversity (as in Fig. 3) (1, 2, 4). Quantifying the specific geological variables that are biologically relevant and distinguishing topographic from geochemical effects remain open challenges for establishing causality. Alternative, process-based explanations should be sought in the interactions between individual mountain regions and other components of the Earth system, especially the atmosphere and the oceans. An emerging conjecture is that mountains are hubs of innovation to such a degree that Earth's biodiversity would have been completely different in the absence of high mountain regions. For example, do mountains in the tropics provide exceptional environmental conditions that encourage fixation of mutations and drive localized adaptive change in plants, in turn driving speciation cascades (the speciation of one group leading to speciation in other groups)? Flenley suggested that the higher ultraviolet B levels on tropical mountain peaks might directly affect DNA, causing a high rate of mutation and leading to evolutionary innovation (40). According to this hypothesis, climatic warm periods that drive species upslope, such as interglacials, should be followed by increased levels of speciation.

A growing consensus holds that models that explicitly incorporate geological and ecological dynamics must take as their starting point the holistic view that all of these processes, acting at different temporal and spatial scales, shape contemporary patterns of biodiversity. The looming challenge is to incorporate these insights within a unified model that generates predictions that can be tested with independent data.

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## Building mountain biodiversity: Geological and evolutionary processes

Carsten Rahbek, Michael K. Borregaard, Alexandre Antonelli, Robert K. Colwell, Ben G. Holt, David Nogues-Bravo, Christian M. Ø. Rasmussen, Katherine Richardson, Minik T. Rosing, Robert J. Whittaker and Jon Fjeldså

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27% closer, respectively, to queen sounds than to those of workers (Fig. 2B) [mean normalized euclidean distances between individual butterflies' and ants' sounds are as follows: pupa-queen  $2.47 \pm$  (SE)  $0.10$ , pupa-worker  $3.03 \pm 0.15$ ,  $t = -3.14$ ,  $df$  87,  $\text{distance}_{\text{pupa-queens}} < \text{distance}_{\text{pupa-workers}}$ ,  $P < 0.001$ ; larva-queen  $2.52 \pm 0.11$ , larva-worker  $3.21 \pm 0.12$ ,  $t = -4.32$ ,  $df$  237,  $\text{distance}_{\text{larva-queens}} < \text{distance}_{\text{larva-workers}}$ ,  $P < 0.001$ ]. The distributions in Fig. 2 also satisfy the concept that the perfect mimic should have maximal overlap with queen acoustics and minimal overlap with those of workers.

Playing recordings of *Maculinea* pupal calls to the same naïve cultures of *Myrmica schencki* workers resulted in enhanced benevolent responses similar to those elicited by queen ant sounds. We found no significant differences toward *Maculinea* pupal and *Myrmica* queen calls in any of the four behaviors scored, and pupal calls elicited six times more instances of royal on-guard attendance than occurred when worker sounds were played (Fig. 3 and table S1) ( $P < 0.001$ ). Recordings of *M. rebeli* larvae induced lower worker responses and, despite eliciting 2.3 times more on-guard attendances than worker calls, did not differ significantly from responses toward worker sounds (Fig. 3 and table S1). We did not play *Maculinea* calls to queen ants but predict that they would provoke rivalry similar to that observed when live *Maculinea* pupae were artificially enclosed with *Myrmica schencki* queens (11) (fig. S1).

We suggest that regional host specificity in *Maculinea* populations is mediated first through chemical mimicry (6, 22); but once the intruder is admitted and accepted as a member of a host society, it mimics adult ant acoustics (particularly queens) to advance its seniority toward the

highest attainable position in the colony's hierarchy. Selection for accurate acoustical mimicry may have been stronger in pupae, which lack the main secretory organs of *M. rebeli* larvae and offer only weak rewards to tending workers.

The young stages of other *Maculinea* species make similar pulsed sounds to *M. rebeli* (12): All differ substantially from those of other studied Lycaenidae, most of which are commensals or mutualists or have no known relationship with ants (12, 23–27). None of the latter mimics the acoustics of associated ants in obvious ways, although the sound of one strongly mutualistic species attracts workers (23–26). Thus, the use of acoustics to signal superior status to ants is unlikely to be a basal trait in the Lycaenidae, although we might expect it in *Phengaris*, the sister genus to *Maculinea*.

Beyond the Lycaenidae, ~10,000 species of ant social parasites may exist (5), particularly among other Lepidoptera, Coleoptera, Diptera, and inquiline ants (1, 6). If acoustics plays the role that we suggest in reinforcing an ant's hierarchical status, it seems likely that this cue has evolved in other social parasites to infiltrate and exploit their societies.

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#### Supporting Online Material

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## Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot

Ana Carolina Carnaval,<sup>1\*</sup> Michael J. Hickerson,<sup>2</sup> Célio F. B. Haddad,<sup>3</sup> Miguel T. Rodrigues,<sup>4</sup> Craig Moritz<sup>1</sup>

Biodiversity hotspots, representing regions with high species endemism and conservation threat, have been mapped globally. Yet, biodiversity distribution data from within hotspots are too sparse for effective conservation in the face of rapid environmental change. Using frogs as indicators, ecological niche models under paleoclimates, and simultaneous Bayesian analyses of multispecies molecular data, we compare alternative hypotheses of assemblage-scale response to late Quaternary climate change. This reveals a hotspot within the Brazilian Atlantic forest hotspot.

We show that the southern Atlantic forest was climatically unstable relative to the central region, which served as a large climatic refugium for neotropical species in the late Pleistocene. This sets new priorities for conservation in Brazil and establishes a validated approach to biodiversity prediction in other understudied, species-rich regions.

Late Quaternary climate fluctuations helped to shape present-day diversity in temperate and boreal systems (1), providing a general context for understanding current patterns of endemism. In the tropics, Pleistocene

refugia models have been dismissed because of conflicting evidence (2, 3) or circularity in identifying putative refugia (4), but historical processes must be invoked to explain regions of high endemism (5, 6). Recent studies from sub-

tropical biomes have usefully employed post hoc palaeoclimate models of species and habitats to provide insights about processes shaping genetic and species diversity (5, 7). Building on them, we first map the palaeodistribution of endemic species to identify temporally stable (refugial) and unstable (recently colonized) regions for species occurrence, which are then validated with multispecies molecular data. Going beyond the traditional species-by-species approach, the molecular analyses contrast the fit of assemblage-level data to the spatially explicit demographic scenarios suggested by the climate-based models.

We apply this approach to one of the world's most species-rich, yet notoriously endangered and understudied ecosystems: the Brazilian Atlantic

<sup>1</sup>Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720–3160, USA. <sup>2</sup>Biology Department, Queens College, City University of New York, Flushing, NY 11367, USA. <sup>3</sup>Departamento de Zoologia, Instituto de Biociências, UNESP, Rio Claro, SP 3526-4100, Brazil. <sup>4</sup>Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, SP 055008-090, Brazil.

\*To whom correspondence should be addressed. E-mail: carnaval@berkeley.edu

rainforest. Originally extending for 1,300,000 km<sup>2</sup> along the Brazilian coast and reaching into Paraguay and Argentina, this biome has been reduced to less than 8% of its range (8). Today's fragments harbor one of the largest percentages of endemic species in the world, with many species and even genera of vertebrates still being described (8, 9). Our ultimate goal is to pinpoint regions for inventory work and habitat protection before we lose a substantial fraction of described and undocumented diversity. The approach differs from previous methods by directly modeling historical processes, as opposed to observed biodiversity patterns (10), with the aim of informing conservation.

We use molecular genetic data from multiple, largely codistributed species to test whether spatial modeling of species-specific Late Quaternary refugia sheds light on historical processes and hence improves prediction of genetic endemism and diversity in tropical Brazil (11). We focus on three common species of tree frogs that are widely distributed along the Brazilian Atlantic forest: *Hypsiboas albomarginatus*, *H. semilineatus*, and *H. faber*. Given their life history traits, amphibians are useful indicators of environmental changes through time (12). Whereas *H. albomarginatus* and *H. semilineatus* occur in low and mid altitudes and are mostly restricted to the evergreen or semideciduous components of the Atlantic Forest in eastern Brazil, *H. faber* has a broader altitudinal range and also inhabits mixed and deciduous areas, occupying interior and coastal sites in the Atlantic Forest south to Paraguay and Argentina (figs. S1 and S2) (13). The comparative phylogeographic approach is a powerful test of assemblage-scale responses to former environmental change and thereby provides a means for critical assessment of the scenarios produced by modeling of species' distributions under palaeoclimates (7).

The palaeomodelling method intersects predicted species' distributions under current conditions and climatic extremes of the Late Quaternary (6000 years before present, or 6 kybp, and 21 kybp) to predict areas of stability (regions in which species are predicted to occupy irrespective of time period) and unstable areas (7, 14). Because the stability maps raise specific hypotheses about regional differences in persistence and hence diversity, they lead to phylogeographic predictions for both individual species and assemblages (co-distributed taxa; Fig. 1). Field sampling is driven by the model predictions to cover both predicted refugia and unstable (recently colonized) areas, particularly emphasizing previously undersampled areas. If the approach correctly predicts current patterns of biodiversity at the regional scale, species should consistently show (i) higher genetic diversity within and among populations in refugia relative to unstable areas, because of long-term persistence and population structure; (ii) genetic signature of population expansion in unstable areas, reflecting multispecies colonization from adjacent refugial regions after the Last Glacial Maximum

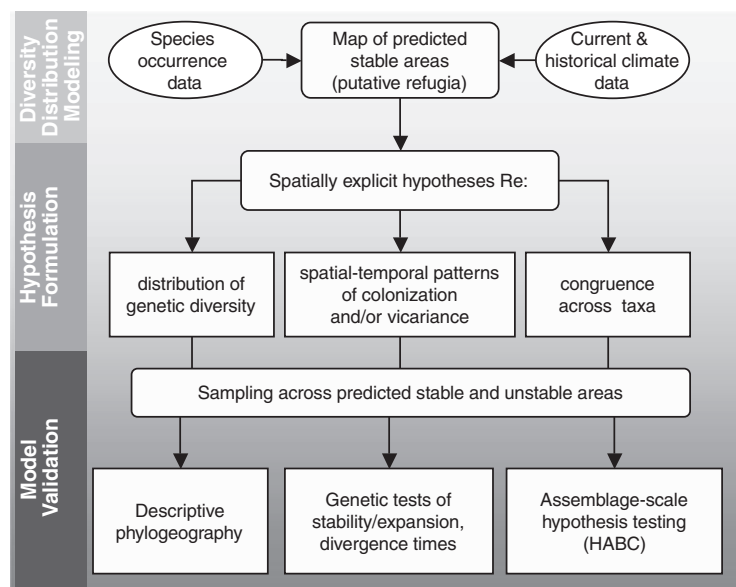
(LGM, 21 kybp); (iii) absence of genetic patterns of isolation-by-distance in unstable areas, given that colonization has been too recent to permit restoration of equilibrium between migration and genetic drift (15); and (iv) strong phylogeographic structure between refugia, reflecting assemblage-wide, long-term population persistence in isolated areas.

Distribution models developed under current climatic conditions accurately predict distributions of each of the target species along the Atlantic rainforest domain [area-under-the-curve (AUC) values (16) 0.968, 0.989, and 0.994; maximum Kappa (17) 0.81, 0.925, and 0.94 in *H. albomarginatus*, *H. faber*, and *H. semilineatus*, respectively (fig. S2)]. Stability maps, depicting the intersection of distribution models for each taxon under current, 6 kybp, and 21 kybp climates, predict for all species a large central refugium throughout the Late Quaternary ("Bahia refugium") (Fig. 2). A second, much smaller refugium is predicted in the northeasternmost portion of the forest ("Pernambuco refugium"). In *H. faber*, a third, southeastern refugium of intermediate size is also predicted ("São Paulo refugium"). This is not surprising, given that this species occupies a broader environmental niche. In contrast to the central and northern regions, populations south of the Bahia or São Paulo refugia appear much less stable, despite the more extensive (preclearing) range of the forest in southern and southeastern Brazil. We hypothesize that these areas received a significant influx of migrants from adjacent, large refugial populations after the LGM. These palaeomodel results are congruent with the fossil pollen record, which documents a replacement of forests by grasslands in the southern Atlantic forest during the LGM (14, 18) and suggests the occurrence of small forest refugia in the southernmost range of

the putative Bahia refugium (19). The results also agree generally with forest models published previously (14), although the central refugium extends farther south in the frog-based models. Such differences are expected because the forest and its associated species may differ slightly in their climatic tolerances and realized niches. In *H. albomarginatus* and *H. faber*, the extension of the predicted São Paulo refugium westward into the neighboring Cerrado biome reflects model overprediction (fig. S2) (14).

Models of habitat stability through fluctuating climates correctly predict patterns of phylogeography in the Brazilian Atlantic rainforest (Fig. 2 and figs. S3 to S5). In all species, high levels of divergence and population structure are observed across refugia (Tamura-Nei corrected distances (20): 4 to 7% between Bahia and Pernambuco refugia, 1% between the nearby Bahia and São Paulo refugia in *H. faber*). Similarly, in all taxa there are multiple, divergent clades within the Bahia region, agreeing with model-based predictions of a large refugium in this area. In *H. faber*, divergent clades are also represented in the São Paulo region, matching predictions of a mid-sized refugium in this area. All taxa show low genetic diversity across the southernmost range of the forest, an area predicted to be less stable by the palaeomodels. Furthermore, mitochondrial DNA (mtDNA) lineages found in this region are shared with adjacent refugia (one in *H. albomarginatus* and *H. semilineatus*, two in *H. faber*).

Metrics of genetic diversity confirm the above patterns (Table 1). In *H. albomarginatus* and *H. semilineatus*, genetic diversity (21) is an order of magnitude larger in the central (Bahia) refugium relative to the less stable (southern) portion of the forest. Diversity of *H. faber* in this southern area is higher than the other species because of the



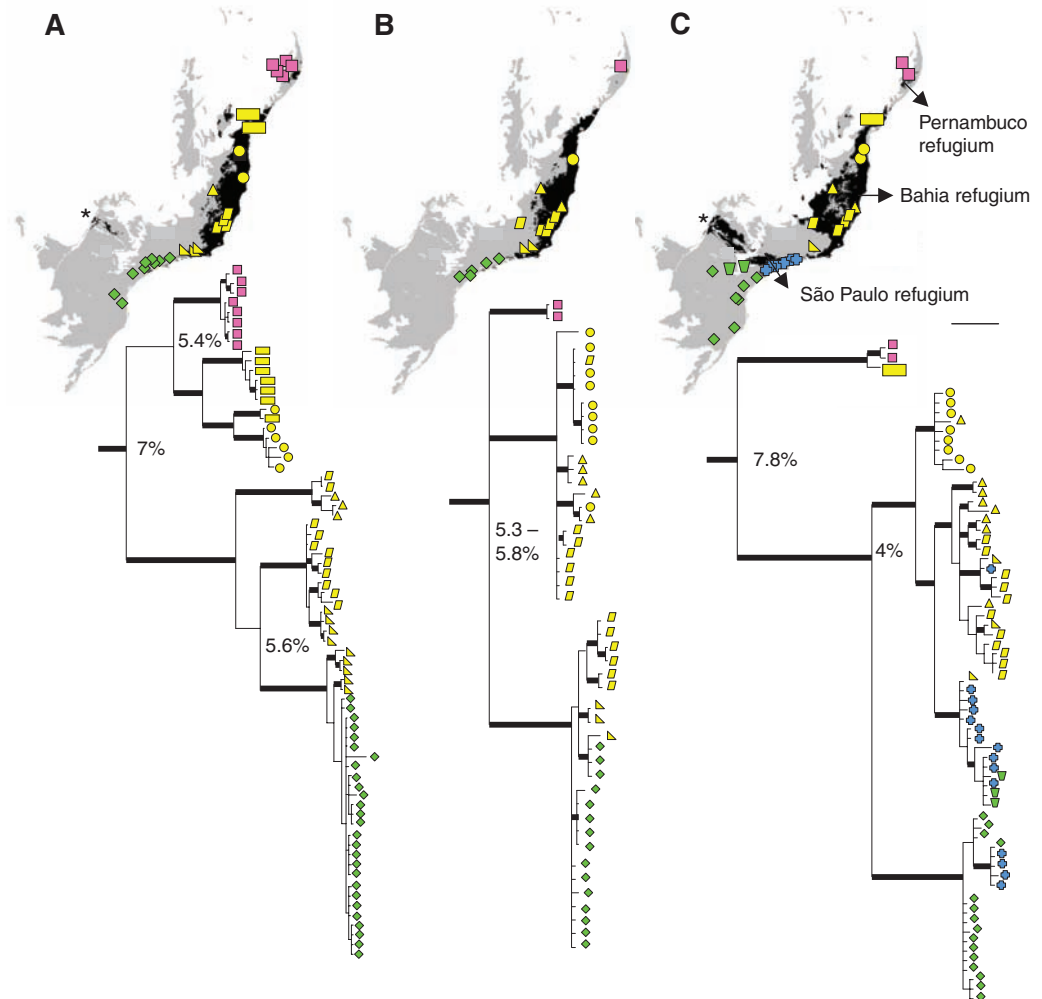
**Fig. 1.** Proposed method of biodiversity prediction. Three stages are involved: biodiversity distribution modeling (top), model-based hypothesis formulation (middle), hypothesis testing and model validation (bottom).

presence of two lineages that co-occur in the adjacent refugia. In all species, average net nucleotide differences across localities (22) reflects high geographic structure within refugia (2.6 to

6.2% divergence). In contrast, sites located outside (south of) the refugia are genetically more similar to each other, although to a lesser extent in *H. faber* (0.1 to 1.6%). Signatures of

population expansion (23) are found in the unstable area for *H. albomarginatus* and *H. faber*, as well as in the Bahia refugia area for *H. faber* and *H. semilineatus*. The lack of signature of

**Fig. 2.** Genetic diversity in putative refugial (stable) versus unstable areas in the Brazilian Atlantic rainforest. **(Top)** Species-specific stability maps; modeled refugia in black. **(A)** *H. albomarginatus*, **(B)** *H. semilineatus*, **(C)** *H. faber*. Note the absence of large stable regions in the southern portion of the forest (south of the Bahia and São Paulo refugia) relative to the central and northern areas. Asterisks denote refugia inferred beyond the current ranges of the target species. Symbols indicate localities sampled for molecular analysis. Scale bar, 400 km. **(Bottom)** The 50% majority-rule consensus Bayesian phylogenetic trees, rooted with sequences from the other two congeneric species studied (root not shown). Thick internodes denote clades with posterior probability greater than 90%. Percentages indicate Tamura-Nei corrected distances between clades (20).



**Table 1.** Population genetic summary metrics used in model validation. *n*, Sample size; *S*, number of segregating sites. The diversity parameter  $\theta$  and mean  $D_a$  across localities are given per base pair (bp). *Hs* test (23) is used to detect population expansion. BA, Bahia; SP, São Paulo refugia. Because predicted refugia were often larger than predicted unstable (recently colonized) areas, *n*, *S*,

$\theta$ , and average  $D_a$  values of the former were obtained not only from the total number of samples, but also from all possible combinations of spatially contiguous localities distributed within the geographic extension of the unstable area. Parentheses encompass minimum and maximum values from subsamples. *P* values in bold highlight statistical significance at 0.05 probability level.

Species	Area	<i>n</i> (min.; max.)	<i>S</i> (min.; max.)	$\theta$ (min.; max.)	Mean $D_a$ (min.; max.)	<i>Hs</i> ( <i>P</i> value)	Mantel's corr. coef. ( <i>P</i> value)
<i>H. albomarginatus</i> (970 bp)	Stable (BA)	36 (13; 23)	207 (81; 155)	0.076 (0.034; 0.072)	0.062 (0.020; 0.082)	-20.546 (0.141)	0.499 <b>(0.001)</b>
	Unstable (south of BA)	27	22	0.003	0.001	-11.498 <b>(0.004)</b>	-0.140 (0.580)
<i>H. semilineatus</i> (718 bp)	Stable (BA)	28 (6; 13)	71 (14; 58)	0.031 (0.009; 0.034)	0.036 (0.007; 0.041)	-17.778 <b>(0.029)</b>	0.054 (0.460)
	Unstable (south of BA)	15	9	0.003	0.004	0.114 (0.357)	0.436 (0.248)
<i>H. faber</i> (771 bp)	Stable (BA)	28 (13; 23)	94 (42; 80)	0.018 (0.012; 0.022)	0.026 (0.001; 0.044)	-38.111 <b>(0.003)</b>	0.803 <b>(0.0003)</b>
	Stable (SP)	15	48	0.023	0.028	-5.981 (0.115)	0.305 (0.221)
	Unstable (south of SP)	18	40	0.015	0.016	-13.255 <b>(0.014)</b>	0.0001 (0.456)

population expansion in the southernmost localities of *H. semilineatus* may reflect low statistical power because of the exceptionally low levels of diversity observed in this species. As predicted, isolation by distance is not observed in unstable regions, but is detected within refugial areas for *H. albomarginatus* and *H. faber*.

The hierarchical approximate Bayesian computation (HABC) method (24) allows us to use data from all three species at once to test for assemblage-wide responses to Late Quaternary climate change. These analyses support both model-driven hypotheses of (i) simultaneous, multispecies colonization of unstable areas from adjacent refugial populations since the LGM, as opposed to long-term persistence of populations in unstable areas, and (ii) assemblage-scale, long-term persistence of populations in isolated refugial areas, as opposed to post-LGM colonization of refugial regions.

To test for assemblage-wide colonization of predicted unstable areas, we group mtDNA sequences from the southernmost refugial sites [population 1 (Fig. 3A)] and from localities in unstable areas south of the refugium [population 2 (Fig. 3A)] to contrast two alternative historical models across the three codistributed species, while allowing the taxon-specific demographic parameters to vary. In  $H_1$ , the long-term persistence model, two contemporary populations split from an ancestral population prior to the LGM (120,000 to 1.2 million years before present, or Mybp, Fig. 3A). In  $H_2$ , the recent colonization model, population 2 is modeled as being colonized from refugial population 1 subsequent to

the LGM (0 to 20 kybp; Fig. 3A). The results indicate that all three species colonized the southern (unstable) areas after the LGM ( $Z_2 = 3$ , the number of species evolved under  $H_2$ ), even when allowing for postisolation migration (Fig. 3, B and C). When Bayes factor is used (25), there is strong support for recent colonization in all three species ( $Z_2 = 3$ ) under the no-migration model [ $B(Z_2 = 3, Z_2 < 3) = 35.16$ ], and moderate support under a postisolation migration model [ $B(Z_2 = 3, Z_2 < 3) = 5.70$ ].

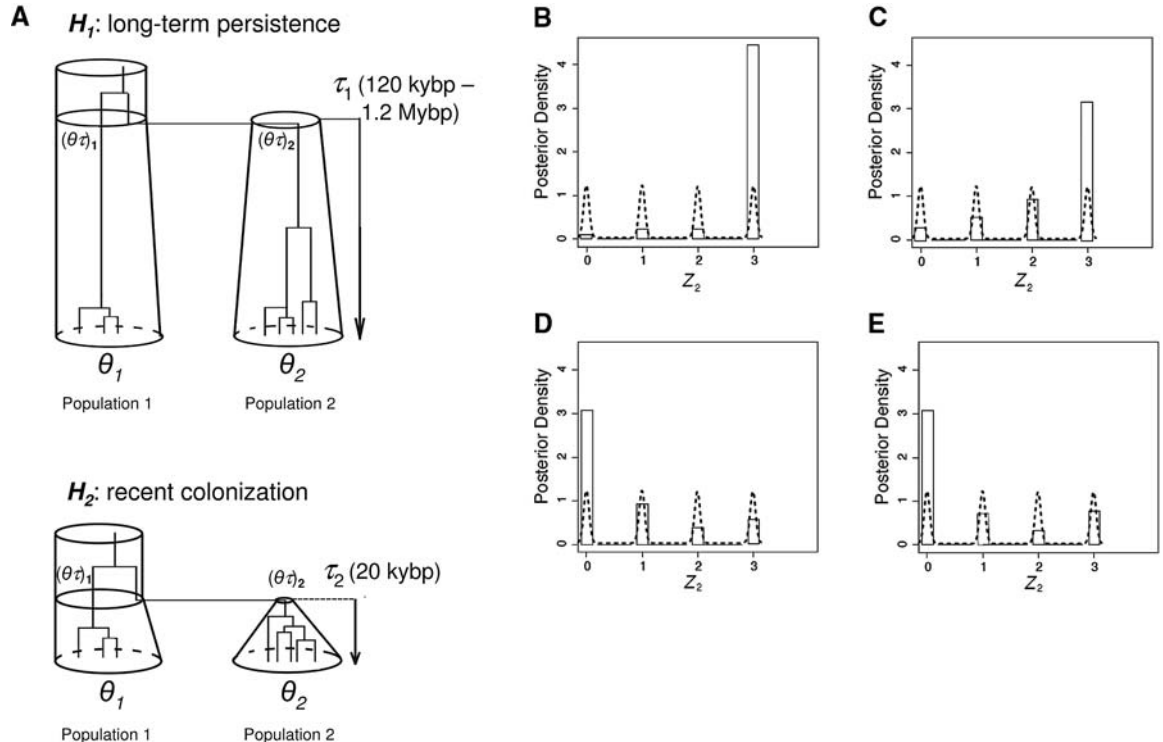
Using the same framework to test for long-term persistence of refugial populations, we compare mtDNA sequences between the predicted Pernambuco refugium [population 1 (Fig. 3A)] and adjacent (northern) populations from the Bahia refugium [population 2 (Fig. 3A)] to contrast alternative historical models  $H_1$  and  $H_2$ . In this case, the HABC results infer long-term persistence of populations in isolated refugia for all three species ( $Z_2 = 0$ , i.e.,  $Z_1 = 3$ ), even when allowing for postisolation migration (Fig. 3, D and E). Using Bayes factor (25), we also detect evidence for stability in both areas under the no-migration model [ $B(Z_2 = 0, Z_2 > 0) = 4.89$ ], as well as under a postisolation migration model [ $B(Z_2 = 0, Z_2 > 0) = 4.84$ ].

Relative to nuclear loci, mtDNA data are more variable and readily collected and often provide key insights into biological response to environmental modification (1). Although single-locus inference can be imprecise in the face of coalescent variance and the possibility of selection (26), our method benefits from a multitaxon approach, while explicitly accounting for the

stochasticity of a single-locus coalescent across taxa. Combining data sets from several codistributed groups into a single hierarchical Bayesian analysis allowed us to estimate congruence across species, while borrowing strength from the full comparative phylogeographic sample (24). This can translate into higher analytical power and be more informative than qualitative comparisons of species-specific analyses. By capturing the historical signal that emerges from larger, combined multispecies molecular data sets, HABC will offer the possibility of looking at patterns of historical community assembly in codistributed nonmodel organisms for which barcode-type DNA sequence information (e.g., mtDNA data) can be feasibly collected.

Collectively, the results identify the central region as a hotspot within the Atlantic rainforest hotspot and a refuge for biodiversity during climatic extremes of the Late Pleistocene. This is not to say that southern areas entirely lacked forested habitats in the late Pleistocene: The existence of species and genera endemic to the southern forests (27), as well as some palaeoecological and genetic evidence (28), offer evidence to the contrary. Rather, the phylogeographically validated palaeomodells presented here show that the central region had much higher stability relative to the south. Forest lizards (14, 29) and birds (30) also show high diversity in the central portion of the biome relative to southern areas, and provide evidence for population expansion in southern regions. This reassures us that the processes uncovered by the amphibian data may be generalized to and help to explain patterns of

**Fig. 3.** HABC analyses. (A) Simulated models  $H_1$  (long-term persistence) and  $H_2$  (recent colonization). In both cases, each species was modeled as two contemporary populations with mutation-drift parameters  $\theta_1$  and  $\theta_2$  that split from an ancestral population at a time  $\tau$  in the past. Ancestral population sizes are represented by  $(\theta_{\tau_1})$  and  $(\theta_{\tau_2})$ ; ybp, years before present. (B to E) Hyperposterior (bars) and hyperprior (dashed) densities of  $Z_2$  (number of species evolved under  $H_2$ ) given data from three codistributed frog species. (B) and (C) Models of refugial sites (population 1) and unstable, southern areas (population 2). (D) and (E) Models of Pernambuco refugium (population 1) and Bahia refugium (population 2). (B) and (D) Postisolation migration not included in model; (C) and (E) postisolation migration included in model.





diversity in other, much more distantly related groups of Atlantic forest endemics.

Because collection efforts, molecular studies, and conservation priorities have been heavily biased toward southern and southeastern Brazil (8, 9, 31), we predict that genetic diversity and narrow endemism in the central corridor of the biome have been substantially underestimated. This is serious, given the higher rate of deforestation in this region relative to the more extensive forests in São Paulo and southern Brazil (9, 31). Not only could much unique diversity be lost, but ongoing habitat destruction could quickly erase the signature of the historical processes that led to it, preventing a full understanding of the mechanisms underlying local endemism and, therefore, impeding more effective conservation measures.

At a broader level, the congruence between model-based demographic hypotheses and joint, multispecies analyses of mtDNA diversity shows that palaeoclimatic niche models and assemblage-scale molecular genetic analyses can be used to forecast spatial patterns of diversity in poorly explored, highly threatened ecosystems. In a world of ever-accelerating environmental changes, this approach can help to guide research and conservation in other global hotspots or similarly complex tropical ecosystems.

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#### Supporting Online Material

[www.sciencemag.org/cgi/content/full/323/5915/785/DC1](http://www.sciencemag.org/cgi/content/full/323/5915/785/DC1)

Materials and Methods

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# Orc1 Controls Centriole and Centrosome Copy Number in Human Cells

Adriana S. Hemerly,<sup>1,2</sup> Supriya G. Prasanth,<sup>1\*</sup> Khalid Siddiqui,<sup>1†</sup> Bruce Stillman<sup>1‡</sup>

Centrosomes, each containing a pair of centrioles, organize microtubules in animal cells, particularly during mitosis. DNA and centrosomes are normally duplicated once before cell division to maintain optimal genome integrity. We report a new role for the Orc1 protein, a subunit of the origin recognition complex (ORC) that is a key component of the DNA replication licensing machinery, in controlling centriole and centrosome copy number in human cells, independent of its role in DNA replication. Cyclin A promotes Orc1 localization to centrosomes where Orc1 prevents Cyclin E-dependent reduplication of both centrioles and centrosomes in a single cell division cycle. The data suggest that Orc1 is a regulator of centriole and centrosome reduplication as well as the initiation of DNA replication.

The assembly of a bipolar, microtubule spindle during mitosis is essential for accurate chromosome segregation. In animal cells, spindle formation is organized by centrosomes, organelles that contain a pair of centrioles surrounded by pericentriolar material (PCM) that need to be duplicated exactly once every cell division cycle, in coordination with DNA replication to maintain genome stability (1). Licensing DNA for replication is a critical regulatory

step involving the origin recognition complex (ORC), the first component for assembly of a pre-replicative complex (pre-RC) at each origin (2). Accumulated evidence supports roles for ORC subunits in addition to licensing DNA replication (3). In particular, human Orc2 subunit localizes to centrosomes, and depletion of Orc2 and Orc3 causes centrosome amplification in mitosis (4).

Several regulators of the DNA licensing machinery have been reported to be involved

in the control of both DNA and centriole duplication (5). Both Cyclin E and Cyclin A, as well as Cdk2 activity, are well-known positive regulators of DNA replication and also promote centrosome duplication (or reduplication) (6–11). Depletion of the DNA replication licensing inhibitor Geminin causes reduplication of both DNA and centrosomes in human cells (12).

In a screen using small interfering RNA (siRNA) for human ORC proteins with roles in centrosome biology, we found that depletion of the largest human ORC subunit, HsOrc1, leads to excess centrosomes (fig. S1 and Fig. 1A). Orc1 siRNA-treated U2OS cells were analyzed for centrosome defects by dual-color indirect immunofluorescence (IF) using antibodies to centrin 2 (stains centrioles) and antibodies to  $\gamma$ -tubulin (stains centrosomes). Seventy-two hours after siRNA treatment, 39.77  $\pm$  3.5% of cells transfected with Orc1-1 siRNA and 25.53  $\pm$  0.3% of

<sup>1</sup>Cold Spring Harbor Laboratory, 1 Bungtown Road, Cold Spring Harbor 11724, NY, USA. <sup>2</sup>Instituto de Bioquímica Médica, UFRJ, 21941-590, Rio de Janeiro, Brazil.

\*Present address: Department of Cell and Developmental Biology, 601 South Goodwin Avenue, University of Illinois at Urbana-Champaign, Champaign, IL 61801, USA.

†Present address: Clare Hall Laboratories, Cancer Research UK, South Mimms, Herts, EN6 3LD, UK.

‡To whom correspondence should be addressed. E-mail: stillman@cshl.edu

## Review



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**Author for correspondence:**

Eli D. Strauss

e-mail: [estrauss@ab.mpg.de](mailto:estrauss@ab.mpg.de)

# The ecology of wealth inequality in animal societies

Eli D. Strauss<sup>1,2,3,4</sup> and Daizaburo Shizuka<sup>3</sup>

<sup>1</sup>Department of Collective Behaviour, Max Planck Institute of Animal Behaviour, Konstanz, Germany

<sup>2</sup>Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

<sup>3</sup>School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA

<sup>4</sup>BEACON Center for the Study of Evolution in Action, Michigan State University, Lansing, MI, USA

EDS, 0000-0003-3413-1642; DS, 0000-0002-0478-6309

Individuals vary in their access to resources, social connections and phenotypic traits, and a central goal of evolutionary biology is to understand how this variation arises and influences fitness. Parallel research on humans has focused on the causes and consequences of variation in material possessions, opportunity and health. Central to both fields of study is that unequal distribution of wealth is an important component of social structure that drives variation in relevant outcomes. Here, we advance a research framework and agenda for studying wealth inequality within an ecological and evolutionary context. This ecology of inequality approach presents the opportunity to reintegrate key evolutionary concepts as different dimensions of the link between wealth and fitness by (i) developing measures of wealth and inequality as taxonomically broad features of societies, (ii) considering how feedback loops link inequality to individual and societal outcomes, (iii) exploring the ecological and evolutionary underpinnings of what makes some societies more unequal than others, and (iv) studying the long-term dynamics of inequality as a central component of social evolution. We hope that this framework will facilitate a cohesive understanding of inequality as a widespread biological phenomenon and clarify the role of social systems as central to evolutionary biology.

## 1. Introduction

Inequality is a general feature of human and non-human animal societies. Most societies exhibit disparities in individual access to resources, physical condition and social relationships. These disparities can be conceptualized as dimensions of wealth inequality, which translate into differences in outcomes such as health, longevity and reproductive success, and ultimately influence variation in fitness. Wealth inequality in different dimensions may be driven by similar underlying processes and have shared effects on outcomes. Social systems may also differ in which dimension of wealth most directly influences individual outcomes. An overarching study of the causes and consequences of wealth inequality facilitates comparisons of the mechanisms underlying variation in outcomes in various societies. Such a perspective can interrogate the myriad potential factors that generate and maintain wealth inequality, scrutinize the consequences of wealth inequality in terms of individual health and reproductive outcomes, or investigate how inequality changes across time within a society.

Researchers in both human- and animal-oriented fields are motivated to understand how wealth inequality arises, is sustained and acts as a mechanism underlying disparities in outcomes, but the general emphasis differs across fields. In the study of modern human societies, research often focuses on how wealth inequality influences health and well-being, with the aim of informing policies that reduce disparities and promote the well-being of as many people as possible. Research in evolutionary anthropology and related fields examines the role of inequality in human evolution, including the evolutionary origins of human

societies and the effects of inequality on fitness in humans [1–7]. In studies of animal societies, the focus often takes an explicitly evolutionary biology perspective, focusing on wealth inequality as a mechanism that generates variation in fitness.

Wealth, inequality and their influences on fitness variation have been considered in different contexts within the fields of evolution and ecology. For instance, a century of work has explored how networks of dominance relationships arise from interactions among group-mates and influence social structure and fitness-related outcomes [8]. Sexual selection theory addresses the causes and consequences of inequality in mating success [9], and studies of reproductive skew examine behavioural constraints on inequality in reproduction [10,11]. Research into collective decision-making explores the causes and consequences of inequality in behavioural decisions [12–14]. Woven into these subfields are theories of kin selection and multilevel selection, which seek to identify how individual wealth influences the indirect fitness of other individuals, and how inequalities within and between groups influence evolution. Thus, much work on social evolution has concerned itself with the causes and consequences of wealth inequality, albeit without explicitly referring to the parallel concepts of wealth and inequality that human-oriented fields have more thoroughly explored. Notable exceptions are work on privatization and property by Strassman & Queller [15] and intergenerational wealth transfer by Smith *et al.* [16]. In this paper, we expand on this prior work to provide a more overarching review of the concepts of wealth and inequality in animal societies, and explore how wealth inequality can be a source of social selection [17–19].

Here we present a research agenda for studying wealth inequality within an ecological and evolutionary context. We synthesize concepts, questions and empirical insights from research in animals and humans to investigate the ecological and evolutionary implications of inequality. We show that this ‘ecology of wealth inequality’ approach presents the opportunity to clarify the role of social systems as central to evolutionary biology, and to reintegrate key evolutionary concepts that have often been perceived as alternatives (e.g. trait evolution, niche construction, extended phenotypes) as different dimensions of the wealth–fitness relationship. We identify four key opportunities in the ecological study of inequality: (i) developing measures of wealth and inequality as taxonomically broad features of societies, (ii) considering how feedback loops link inequality to individual and societal outcomes, (iii) exploring the ecological and evolutionary underpinnings of what makes some societies more unequal than others, and (iv) studying the long-term dynamics of inequality as a central component of social evolution. In each section, we review existing work and highlight areas requiring additional empirical and theoretical attention. We aim to motivate a cohesive interdisciplinary approach to understanding inequality as a widespread and diverse biological phenomenon.

## 2. What are wealth and inequality in animal societies?

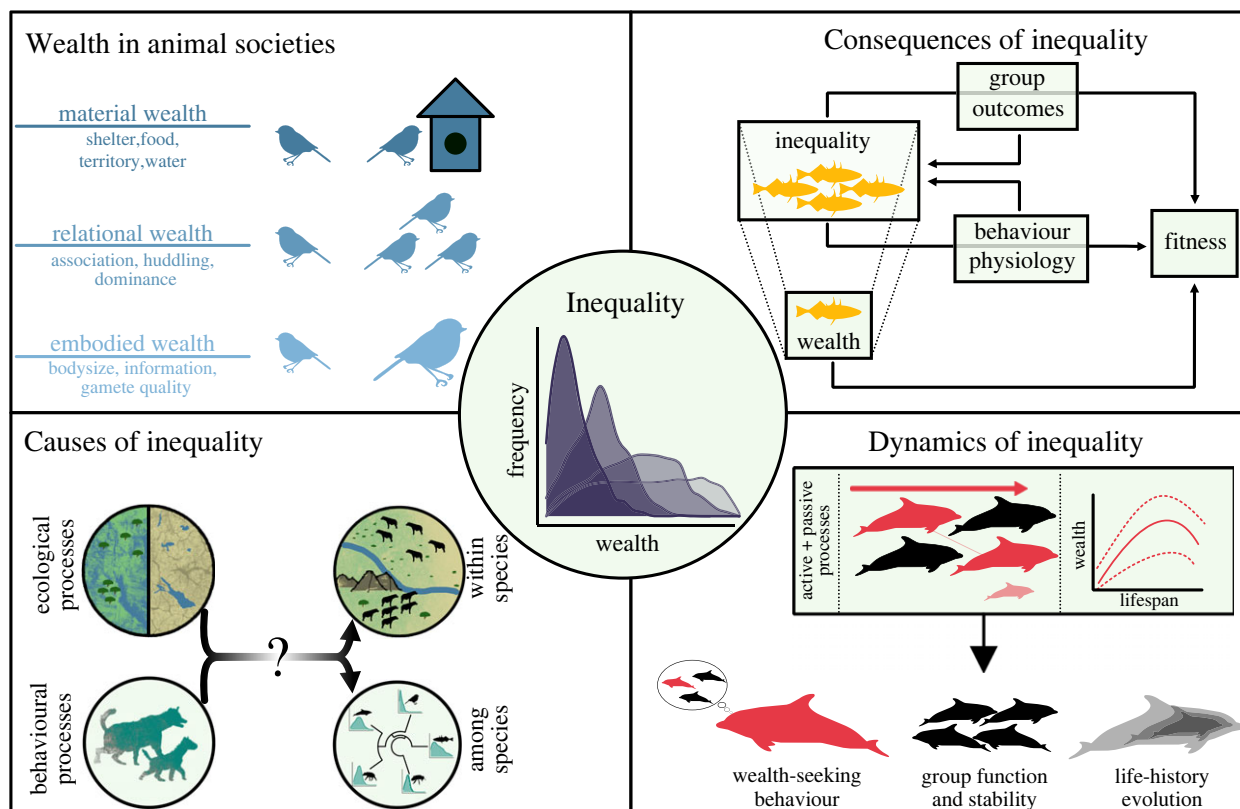
Non-humans do not have bank accounts, so how can they be wealthy? Economists and evolutionary anthropologists have long known that wealth can take many forms [20,21]. Wealth manifests in many *currencies*, or quantities of attributes or possessions that impact an individual’s access to

‘valued goods and services’ [22]. Although the currencies of wealth are numerous, they can be pooled into three super-seeding categories (here ‘*aspects*’; figure 1, top left) [4,22,23]. *Material wealth* denotes extrasomatic currencies such as money, land or livestock. *Relational wealth* consists of social connections, often measured as ties in a network of relevant social interactions or relationships such as food sharing, prestige or cooperative hunting. Finally, *embodied wealth* refers to attributes of individuals, such as size, strength or knowledge.

This framework reveals how animal societies are also structured by multiple dimensions of wealth. These same three aspects—material, relational and embodied wealth—are key elements of animal societies and map clearly onto established concepts in ecology and evolution, such as constructed/defended niches, social niches and phenotypic traits. Material wealth currencies include defensible resources such as food items, nest sites and territories, as well as ‘constructed’ resources such as food caches, shelters and nest decorations [15,16]. For instance, material wealth is prominent in acorn woodpeckers (*Melanerpes formicivorus*), which invest heavily both in granary construction (the work of generations of woodpeckers) and in the collection and storage of acorns within the granary [24]. Material wealth may also take the form of empty snail shells occupied by hermit crabs (*Pagurus longicarpus*)—resources that are unequally distributed in quality and directly affect fitness outcomes [25]. Relational wealth describes an individual’s social niche [26], encompassing social relationships and interactions such as grooming, huddling or dominance. Considerable evidence points to the impact that relational wealth has in human and non-human animal societies [6,27,28]. For example, social alliances influence rank and fitness in spotted hyenas (*Crocuta crocuta*) [29]. Embodied wealth is made up of phenotypic currencies such as body size, fat reserves, sperm quality, ornament size, display quality or information. Classic examples of embodied wealth are condition-dependent signals, such as the male house-finch’s (*Carpodacus mexicanus*) bright red plumage [30]. These different aspects of wealth operate concurrently, and biological market theory provides a framework for understanding exchanges in a wealth of different currencies [31].

Wealth inequality describes the spread and skewness of distributions of wealth (figure 1, centre circle) in these different dimensions (box 1). The scale at which inequality is assessed can be tuned flexibly according to the question and the study species. For instance, one can measure inequality among individuals in a society or social group, or among individuals in a population consisting of multiple social groups. When wealth operates at the group level (e.g. group territories, shared food caches), wealth inequality among groups can be assessed at the population level.

There is broad consensus in evolutionary theory that material and relational wealth (i.e. constructed and social niches) can influence fitness, drive adaptation and contribute to evolutionary change [44]. Existing biological concepts also describe the transmission of wealth across generations via mechanisms of genetic and epigenetic inheritance, ecological inheritance [45] and social inheritance [46]. Intergenerational transmission of wealth may affect ‘privilege’ as a source of inequality in animal societies [16]. Exploring evolutionary themes such as niche construction and social inheritance from the lens of wealth inequality could provide clarity to debates on how to integrate these dynamics in evolutionary theory [47,48]. Specifically, we argue that the patterns of distribution



**Figure 1.** A schematic of the ecology of inequality. Centre circle: inequality describes the distribution of wealth among individuals, which can be measured using metrics borrowed from economics (box 1). Top left: wealth is taxonomically broad and occurs in many currencies, grouped into three aspects. Top right: inequality emerges from individual wealth through bottom-up causation and has a top-down influence on individual outcomes, both directly and via its effects on group outcomes. These effects are independent of the effects of wealth, but can feed back to influence wealth and inequality. Bottom left: multiple ecological (e.g. food/water distribution) and behavioural (e.g. wealth inheritance) processes are hypothesized to influence the amount of inequality in societies, but it is less clear at what scale this influence occurs or to what degree these processes operate across species. Bottom right: inequality is dynamic. Active and passive processes produce changes in wealth within an individual's lifetime and across generations, leading to typical wealth trajectories over the lifespan. The amount, timing and direction of wealth trajectories are expected to exert selection on individuals to optimize their experienced costs and benefits of sociality. (Online version in colour.)

### Box 1. Measuring inequality.

Here, we provide a brief introduction to the methods for measuring inequality, intended to introduce the reader to what is an extensive body of literature in economics. Distributions can differ from pure equality in numerous ways [32–35]. When empirical wealth distributions are well described by the functional form of one or more distributions, inequality can be described analytically via the parameters specifying the distribution [36]. Alternatively, inequality can be measured by summarizing the amount of wealth held by individuals in a certain quantile (e.g. the proportion of total wealth held by the wealthiest 10% [37]) or by comparing the wealth of individuals in different quantiles. Finally, 'index' approaches summarize inequality into a single numerical index. The Gini index is the most commonly used metric of inequality, and although most often applied to income, it has also been used to study inequality in distributions of monetary wealth [38], land ownership [23], faculty production by universities [39], body size [40], plant sizes [41] and hermit crab shell sizes [25]. Because a single parameter cannot fully summarize the shape of a distribution, different indices are sensitive to different features of unequal distributions, so caution is warranted when indices disagree [32]. Finally, it is important to note that most of these methods were developed to describe inequality in large nation-states, and methodological challenges remain to facilitate comparative approaches to inequality in smaller societies such as those found in non-human systems [34,35,42,43].

of each aspect of wealth matter, and understanding the structural properties of wealth inequality is key to evolution. For example, niche construction may play a key role in evolution only when the intergenerational transmission of material wealth fundamentally alters how fitness is related to embodied aspects of wealth.

### 3. What are the consequences of inequality?

Inequality can influence outcomes for individuals directly or by impacting group outcomes (figure 1, top right). There is a

long history of sociological research describing different types of effects of wealth inequality (reviewed in [49]). Most directly, variation in individual wealth may translate into variation in outcomes, and such effects may be linear or non-linear. From an evolutionary ecology perspective, simple effects of wealth on fitness represent selection on various aspects of wealth, such as traits (embodied wealth), resource acquisition and defence (material wealth), or social behaviour (relational wealth). However, sociological approaches to wealth inequality also reveal other effects that may be

relevant to non-human societies. On top of simple wealth effects on outcomes, individuals are influenced by inequality in the distribution of wealth such that two equally wealthy individuals living in societies with different levels of wealth inequality might experience divergent outcomes. Here, we highlight three such effects: (i) the overall level of inequality at the group or society level may have effects beyond an individual's wealth; (ii) behavioural responses to inequality, and (iii) effects of inequality on group persistence or collective action.

Wealth and wealth inequality impact individual health and well-being [28,50–52]. In humans, more unequal societies are often associated with negative individual and societal outcomes [53,54]. An evolutionary comparison across primates, including humans, reveals that life-expectancy increases with lifespan equality, further indicating that inequality covaries with individual outcomes [55]. Inequality negatively impacts health and well-being through behavioural changes [56] or psychosocial stress [57]. In humans, inequality-induced stress is more extreme in societies that are more unequal, even for individuals of high social status [58]. Status-induced stress can affect both low- and high-wealth individuals, and who experiences most stress can depend on the dynamics of the social system [51,59,60]. Overall, widespread association between wealth inequality and individual outcomes supports the hypothesis that living in the context of wealth inequality is a 'fundamental cause' of a suite of negative outcomes [28,56,61].

Individuals attend to inequality within their societies and alter their behaviours accordingly. Experiments in primates, corvids and domestic dogs suggest that the perceived value of a resource is influenced by an individual's observations of the value of the resources their group-mates receive [62]. Individuals often then alter their social behaviour, for example by punishing individuals that receive the higher valued resource [63]. Similarly, subordinate queens of *Polistes fuscatus* wasps greatly increase aggression towards dominants when they perceive that dominants are claiming too unequal a share of reproduction [64]. In humans, an individual's wealth influences their perceptions about the degree of inequality in society [65] and their status-seeking behaviour [66]. In many species, individuals use social information about their status relative to their competitors when making decisions about how and with whom to compete [67]. In sum, intra-group competition and inequality are linked by a feedback loop involving individual perception of their own social status, the social status of others and the amount of inequality in the group. To understand this feedback loop, we should continue to explore how individuals perceive inequality, and how their response to inequality affects social structure. Systems where signals of wealth can be manipulated independently of actual wealth provide a means to experimentally manipulate perceived inequality.

Inequality can influence group outcomes such as group persistence and collective action. Reproductive skew theory [10,11] addresses how inequality in reproduction can affect the productivity or persistence of the group. Inequality can also influence a group's ability to cooperate or achieve collective action. In cooperation experiments with chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and cotton-top tamarins (*Saguinus oedipus*), evidence suggests that species that divide the rewards of cooperation more equally are more likely to show cooperative behaviour [68,69]. Theoretical and empirical studies of collective action problems

(e.g. public goods game) suggest that inequality has complex and often unpredictable effects on cooperative behaviour [70–77]. However, a rough pattern emerges in the literature suggesting that the effect of inequality on cooperation might depend on the type of wealth under consideration. In studies where individuals vary in the resources they can invest in cooperation (i.e. material wealth), inequality typically reduces cooperation [70–72]. However, inequality in social influence can promote cooperation by eliminating free-riders and overcoming coordination challenges [73–77]. Other evidence suggests that inequality can influence group outcomes by improving or impeding the function of groups, for instance by altering costs of coordination, resilience to variable environmental conditions, or ability to compete with other groups [73,75,78,79]. For example, burying beetles (*Nicrophorus nepalensis*) invest more in cooperation in the face of interspecific competitors [80]. A complex relationship between inequality and environment may explain global patterns in the evolution of cooperation: in both *Polistes* wasps and cooperatively breeding birds, the evolution of cooperative groups is associated with the environmental conditions that may increase the need for collective action (e.g. unpredictable environments: [81–83]). Overall, the complex results from theoretical studies suggest a need for empirical work on the links between inequality, individual outcomes and group function in animal systems.

#### 4. What are the causes of inequality?

Multiple behavioural and ecological processes have been hypothesized to influence the amount of wealth inequality within societies, but the extent to which these mechanisms explain variation within versus among species is not fully clear (figure 1, bottom left). Some aspects of inequality seem to be relatively flexible, whereas others are more constrained. For example, in a population of olive baboons (*Papio anubis*) in Kenya, a mass mortality event prompted a long-term shift towards a more tolerant society with more equally distributed stress burdens, perhaps as a result of the death of the individuals that competed most intensely for high status [84]. However, a comparative network motif analysis of dominance hierarchies across many species suggests strong constraints on their structure related to transitivity of dominance relations [85]. Furthermore, in macaques, a suite of behaviours related to inequality in within-group conflict covary across species, producing macaque societies with different 'social styles' and suggesting potential phylogenetic constraints on wealth inequality [86,87]. More longitudinal and phylogenetic studies will be crucial to advance our understanding of plasticity and constraint in inequality across species.

What behavioural and ecological mechanisms influence variation in inequality within and among species? Ecological conditions—such as the patchiness, density and defensibility of resources—have long been hypothesized as a driver of material wealth inequality [1,2,9,88] (but see [89,90]). Additionally, inequality may be influenced by behavioural traits such as levelling coalitions used to control would-be dominants [91], aversion to unequal payoffs [62], preferences regarding perceived inequality [92], status-seeking behaviour [93], visibility of wealth [94] and cognitive processes relating to social competition [67]. Individuals can actively suppress

the wealth of others, as is seen in growth suppression by many fish [95] or the interruption of social bond formation in ravens (*Corvus corax*) [96], or subordinates may voluntarily reduce their own wealth to avoid conflict with group members [97]. Self-reinforcing dynamics—where ‘rich-get-richer’ feedbacks lead wealthy individuals to gain more wealth—can also influence the amount of inequality in societies [98] (see §5). Finally, these behavioural and ecological mechanisms interact. For example, the evolution of male coalitions in primates is explained by resource defensibility [99], and in vulturine guineafowl (*Acryllium vulturinum*), monopolization of clumped resources by dominants can lead to more egalitarian group movement decision-making [13].

Although drivers of inequality may differ among species or wealth aspects, some hypothesized causes of inequality are expected to operate across contexts. For example, the social transfer of wealth is one hypothesized driver of inequality that is likely to operate widely [3,4,16]. In a broad survey of human societies with diverse production systems, the increased fidelity of intergenerational transmission of wealth was associated with more extreme inequality [4,22]. In non-human animals, social inheritance of territory [100,101], knowledge [102,103], social relationships [46] and food caches [24] could provide ample contexts in which to test this hypothesis in diverse systems [16]. For instance, the social inheritance of dominance status in spotted hyenas and Old-World primates may drive inequality in dominance among lineages [29]. In fact, the widespread transmission of wealth across generations points to the evolutionary importance of non-genetic inheritance [45] and selection in response to multigenerational processes [104]. Another broadly operating hypothesized driver of inequality is intergroup conflict. When unequal groups are more effective or willing competitors, selection for success in intergroup conflicts can lead to increased within-group inequality in influence during collective action [79,105,106], and these leaders can also use their influence to increase inequality in other dimensions of wealth [107]. Here there is potential for positive feedback when the individuals that benefit most from intergroup conflict are also effective initiators of these conflicts, as seen in humans and banded mongoose (*Mungos mungo*) [108,109]. Finally, environmental stressors arising from climate change are expected to impact many species, highlighting another potentially broadly acting driver of inequality that we need to better understand. Studying shared processes influencing inequality in diverse wealth currencies and species is key to understanding the evolution of inequality and its role in societies.

## 5. How does inequality change over time?

Inequality is dynamic: neither the level of inequality nor an individual’s wealth is fixed, and both can change over short or long timescales (figure 1, bottom right). One avenue for understanding these dynamics is through the economic concept of *social mobility*, which describes the dynamics of wealth measured at the individual or lineage level. Aggregating these measures across members of a social group reveals the society-level tendency for individuals or lineages to gain or lose wealth over time, producing more rigid or fluid societies. By integrating over time, social mobility mediates the link between inequality measured at a given time point and the processes or outcomes occurring over individual lifetimes.

Social mobility can vary in the timescale at which it occurs and the processes by which it arises. Intra- and intergenerational mobility classify the generational scale at which mobility occurs. *Intragenerational mobility* describes the degree to which individual wealth changes, producing wealth trajectories over the lifespan. *Intergenerational mobility* refers to the change in wealth within lineages across generations and is the type of social mobility most often studied in humans [110–112]. Examining the correlation between parents’ and offspring’s wealth provides an empirical measure of the extent to which an individual’s position in society is malleable versus predetermined [113]. Increasingly, researchers are expanding the study of intergenerational mobility to include multigenerational effects, such as the effects of grandparents or other more distant kin [114,115].

Processes influencing social mobility can be active or passive: *active mobility* occurs when an individual’s wealth changes with respect to their group-mates by reversing the wealth-ordering of individuals, whereas *passive mobility* occurs as a result of demographic processes such as births and deaths [116]. These demographic processes frequently produce gradual changes that have direct and indirect effects on social structure by removing and replacing individuals and altering existing social relationships [117]. In some cases, demographic changes can push societies over tipping points, or precipitous shifts in social structure that can show hysteresis [118]. Revolutions [119], mass mortality [84,119,120], group fissions [121], the arrival or loss of certain individuals [122–124] and expulsions of group members [125] are examples of active and passive processes that could produce precipitous changes. For instance, social perturbation experiments in captive fish, primates and mice demonstrate how removal of high-status individuals can lead to rapid behavioural, physiological and cognitive changes in other individuals [122–124].

The long-term additive combination of social mobility produces *long-run inequality*, which describes equilibrium patterns of inequality around which a society fluctuates [37,126], assuming such an equilibrium state exists. Understanding where a society sits relative to its expected equilibrium state will require long-term studies in the order of multiple generations. In turn, such work creates opportunities for exploring the forces that lead societies to deviate from or return to their equilibria. This long-run perspective could help us understand when and why societies may have distinctively low social mobility, leading to ‘durable’ inequality [127], or inequality that persists across individuals, time or generations [1]. Durable inequality can give rise to social classes, where individuals of different classes form social networks with different structures, face different mortality sources and cope differently with stressful conditions [60,128,129]. One process producing durable inequality is self-reinforcing dynamics, where already wealthy individuals accrue disproportionately greater wealth [130–133]. Preferential attachment and ‘rich-club effect’ models of social relationships demonstrate how relational wealth can show such self-reinforcing dynamics [134,135]. Frequency-dependent or fluctuating selection may be a counterforce that inhibits the buildup of durable inequality by altering fitness landscapes [136].

Patterns of social mobility may influence the evolution of a wide suite of behavioural strategies such as tolerance and wealth-seeking behaviour, as well as life-history traits related to pace of life (figure 1, bottom right). When upward intragenerational mobility is achieved through active processes,

selection is expected to favour individuals that challenge their group-mates, whereas conflict avoidance and tolerance should be favoured in species where upward intragenerational mobility is achieved through passive processes (e.g. social queuing; [137]). Low intergenerational mobility is expected to amplify selection on traits related to intragenerational mobility, as any changes within a generation are likely to persist and influence future generations. This hypothesized selection driven by social mobility reflects ways in which patterns in the dynamics of social structure can feed back to influence the evolution of individual traits [138], including life-history traits.

Contrasting hypotheses about the influence of social mobility on the stability of social groups highlights potential tradeoffs in the evolution of social structure. On the one hand, some have suggested that upward social mobility is crucial for long-term group stability, as individuals are expected to leave societies where they have no opportunity for wealth acquisition [126]. This pattern of upward mobility is prominent in societies where individuals ‘queue’ for wealth, such as in long-tailed manakins (*Chiroxiphia linearis*) [139], where individuals move up the queue through passive processes (e.g. death of wealthier individuals) [137,139,140]. By contrast, overly frequent active mobility can cause social instability, which is associated with negative consequences for individuals and societies [51,141–143]. These contrasting perspectives emphasize the need for theoretical and empirical work that generates and tests hypotheses about the link between social mobility and the functioning of societies in diverse species.

## 6. Conclusion and future directions

A key question in ecology and evolution is how the structure of groups arises and impacts the individuals that compose them [138]. Inequality in the distribution of wealth—be it relational, material or embodied—is a group-level feature that is hypothesized to impact individual and group outcomes. Here we coalesce disparate studies of inequality in biological systems into a research framework addressing inequality across ecological and evolutionary contexts and identify three overarching research foci.

First, how does inequality impact individuals beyond the simple effects of individual wealth? Evidence suggests that individuals attend to the amount of inequality within their societies, and that inequality *per se* may have adverse effects for individuals. Here, theoretical work has outpaced empirical work, and examining the impacts of inequality on individual and group outcomes in non-human systems will be fruitful. Experimental studies of inequality in laboratory populations is a promising tool for disentangling the effects of inequality from the effects of wealth. The recent surge in work on social dimensions of health and lifespan in non-human animals promises to shed light on potential avenues by which inequality influences fitness [28].

A second broad aim of the ecology of inequality is to understand the forces that cause inequality, both in the

short term and at evolutionary timescales. Some aspects of inequality can be plastic—even sensitive to the behaviour of a single individual—whereas other aspects of inequality are evolutionarily constrained. The interplay between behavioural processes and environmental conditions (e.g. resource scarcity and competition) fundamentally shapes wealth inequality. Biogeographical and phylogenetic approaches may be useful here for identifying ecological and evolutionary patterns in wealth inequality at a global scale. Finally, feedback loops operating across species and types of wealth might explain why inequality is such a common feature of societies across the animal kingdom.

Third, it is crucial to take a dynamical perspective on inequality to understand selection on individual traits, long-term patterns in inequality, and the stability and persistence of groups. Social mobility—or changes in wealth—can occur owing to various processes and at different timescales, leading to higher-order patterns in inequality among individuals and their descendants, such as social classes or family dynasties. However, very little is known about the existence or implications of these higher-order patterns in inequality in non-human systems. Long-term studies that track groups and their constituents over multiple generations are uniquely situated to address this knowledge gap. Furthermore, we call for theoretical models that explore how lifetime patterns of social mobility impact the evolution of life-history traits and wealth-seeking behaviour.

Inequality is a curiously widespread feature of societies. The framework presented here offers a way forward for exploring the causes of inequality, its impacts on individuals and its role in social evolution. The framework allows inequality to be understood in specific contexts while also providing a means for comparative insight and the identification of general features of inequality operating across species and dimensions of wealth. This approach at once strengthens biological and sociological fields by integrating perspectives and facilitating the exchange of ideas, paving the way for new insights into ecological and evolutionary forces impacting social organisms.

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Both authors gave final approval for publication and agreed to be held accountable for the work performed herein.

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