The human dimension of biodiversity changes on islands

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Islands are among the last regions on Earth settled and transformed by human activities, and they provide replicated model systems for analysis of how people affect ecological functions. By analyzing 27 representative fossil pollen sequences encompassing the past 5000 years from islands globally, we quantified the rates of vegetation compositional change before and after human arrival. After human arrival, rates of turnover accelerate by a median factor of 11, with faster rates on islands colonized in the past 1500 years than for those colonized earlier. This global anthropogenic acceleration in turnover suggests that islands are on trajectories of continuing change. Strategies for biodiversity conservation and ecosystem restoration must acknowledge the long duration of human impacts and the degree to which ecological changes today differ from pre-human dynamics.

Globally, human activities dominate ecological systems (*1*, *2*) and are considered the main drivers for accelerating contemporary ecosystem transformation (*3*–*6*). The pressing need to evaluate the extent and dimensions of human impacts and the desire to restore “wild” systems have sparked controversy concerning the value of establishing pre-human baselines (*7*–*9*) and about the nature and timing of the onset of the Anthropocene (*10*–*12*). Archaeological and other paleodata on human impacts in continental systems reveal an increasingly human-transformed planet intensifying around the end of the Pleistocene (*2*, *13*, *14*). The lengthy time frame of human modification of ecosystem dynamics in continental contexts, spanning periods of substantial post-glacial climate change, complicates the definition of pre-human baselines and hinders the investigation of natural ecosystem processes (*15*, *16*).

In contrast to continents, most remote oceanic islands were colonized by people relatively recently, within the past 3000 years, when climates were similar to present conditions (*17*). The recent nature of human settlement means that the archaeological, paleoecological, and climate records are often more precisely resolved on well-studied islands compared with continents and are potentially more relevant for understanding remnant ecosystems and informing conservation and ecosystem restoration agendas. Therefore, island ecosystems provide opportunities to quantify the critical ecological transition from pre-human to human-dominated ecosystems (*4*, *15*), and allow anthropogenic impacts on ecosystems to be placed within the context of long-term pre-human ecological dynamics (*16*–*20*). Although numerous studies have documented the timing, waves, and processes of species extinctions that accompanied human arrival on islands (18–24), paleoecological data networks now allow systematic quantification of ecosystem transformations on islands globally. Here, we analyzed fossil pollen time series for multiple independent islands from all the major archipelagos and oceans and across latitudes, using a breakpoint regression approach to test for altered rates and directionality of pollen, and thus vegetation compositional turnover, connected with human colonization (25) within an overall time frame of the past 5000 years. These time series of millennial-scale dynamics allow the assessment of whether the rates of vegetation compositional change consistently accelerated across multiple islands after initial human arrival. Our method uses ordination analyses to characterize the major gradient of compositional variation in the pollen data for each island, quantifying the mean rate of change through time before and after human arrival (Fig. 1), thereby allowing us to assess how human populations affected islands differently from natural perturbations (23).

Our results show that human arrival systematically accelerated directional compositional change in island ecosystems (Figs. 1 and 2). Rates of pollen compositional turnover increased after human arrival by up to a factor of 11, with large differences amongst islands (i.e., a median of 10.7 times higher turnover after human arrival, with a mean of 20.8 ± 26.5 times higher turnover). This acceleration is a globally consistent pattern observed on 24 of 27 islands independent of current and past island area, latitude, isolation, and elevation of the sampling site [(Fig. 3, B to G, and Tables S3 and S4 (25)]. Islands that were settled more recently, such as the Poor Knights archipelago in New Zealand (13th century) (19) and the Galápagos Islands (16th century) (26), show a steeper increase in the rate of turnover change ($P = 0.008$, $R^2 = 0.22$; linear regression with log-transformed arrival time; Fig. 3A)) than on islands where humans arrived >1500 years ago [e.g., New Caledonia (27) and Fiji (28)]. This indicates either that the islands settled earlier were more resilient to human arrival or, more likely, that the recent major compositional turnover observed is explained by introduced species, land-use practices, and technology deployed by later settlers being more transformative than those of earlier settlers. In addition, those islands colonized >3000 years ago appear to show some declines in rates of compositional turnover toward the end of the sequence, although there are too few cases (n = 5) to draw firm conclusions.

For many islands, the model implementing a prescribed breakpoint at the time of human arrival closely fits the observed patterns in compositional turnover (Fig. 1). Human arrival estimates fall within the 95% confidence intervals of the optimal breakpoints (representing the greatest change in turnover in each record) for 41% of islands. Human arrival times are within 500 years of the optimal breakpoint for 70% of islands and within 1000 years for 81% of islands (median 329 years compared with 953 for randomized data simulations; Table S5 and Fig. 2). There is no tendency for optimized breakpoints to be systematically earlier or later than estimated human arrival time (*t*-test with null model of mean difference being 0, $P = 0.27$). A systematic difference would have either indicated earlier human arrival or delayed human impact. On some islands, initial human arrival is not associated with a major shift in turnover [Figs. 1 and fig. S1 (25)]. These results might reflect the specific local characteristics of the study site. For example, on La Gomera (Canary Islands), the sedimentary sequence was collected at an elevation of 1250 m above sea level in one of the largest remnant areas of laurel forest, where paleoecological analyses showed no evidence of human impacts (29). On other islands, e.g., Hispaniola, shifts in vegetation turnover differed from the time of human arrival, as estimated based on archaeological or historical sources, but the rate of directional change increased (Fig. 1).

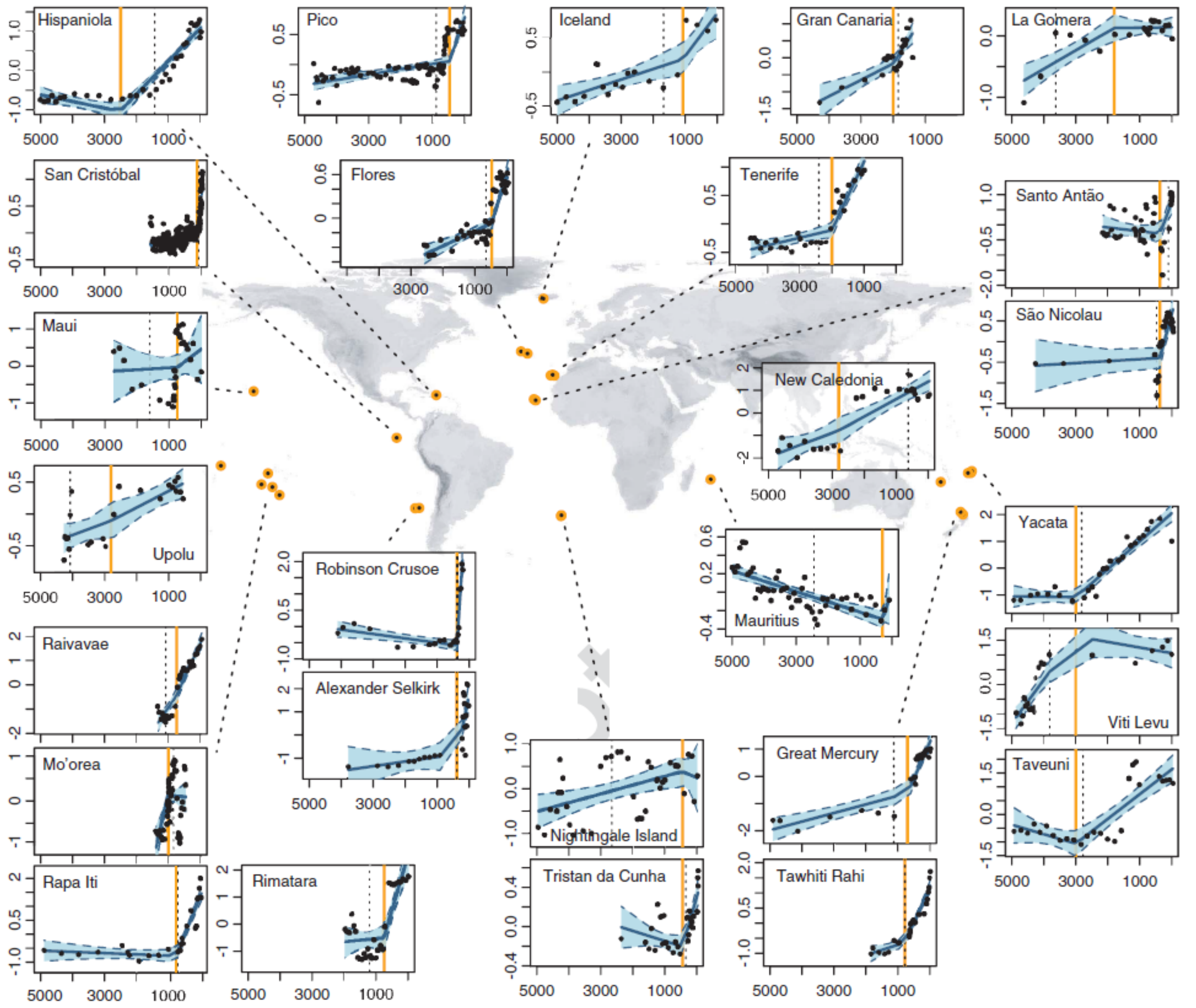

Fig. 1. Human arrival accelerated compositional turnover on islands. Global analysis of rate of palynological and thus vegetation compositional turnover (slope of the line) for 27 representative fossil pollen records from sedimentary sequences on islands. The *x*-axes represent calibrated years before present (i.e., years before 1950) calculated using Bayesian age-depth models for each island (*25*). The *y*-axes represent the major gradient in pollen composition quantified by the ordination axis 1 scores of separate detrended correspondence analyses (DCAs) of each sequence. The units are measured in DCA axis scores, which approximate the standard deviation of pollen taxon compositional turnover (SDptt), with an SD of 4, corresponding roughly to 100% compositional turnover. These plots show results of breakpoint analyses of the rate of compositional turnover with the date of recorded human arrival as the prescribed breakpoint. The recorded date of human arrival is indicated by the vertical orange lines (see Table S3 for details). Scaling varies among panels. Shaded areas (blue) depict 95% confidence intervals of the models. A second continuous breakpoint analysis detecting the major statistical change point in turnover rate intrinsic was applied to the data. This "optimized breakpoint" is indicated by the vertical dashed black lines.

Our analysis also shows that ecological change is an integral part of island systems, with changes observed both before recorded human arrival [directional change in composition measured in standard deviations of pollen taxon turnover (SD_{ptt}) per 100 years: median turnover 1.7×10^{-2} SD_{ptt}/100 year and mean turnover $4.0 \pm 6.8 \times 10^{-2}$ SD_{ptt}/100 years and after human arrival (median turnover 14.7×10^{-2} SDptt/100 years and mean turnover $23.3 \pm 29.8 \times 10^{-2}$ SD_{ptt}/100 years)] (Fig. 2). Results show that the rate of directional turnover before human arrival was slower, in contrast to human agencies of change. Natural drivers of ecosystem change on islands, operating before and alongside humans include: volcanic activities, fire, climate change (episodes such as the "Little Ice Age"), earthquakes, extreme weather events (e.g., droughts and cyclones), and sea-level fluctuations (20, 30, 31). Although not measurable with the precision necessary to include formally within our analysis, volcanic activities and natural climate fluctuations have likely not increased over the analyzed time frame across the islands studied and thus cannot explain the systematic increase and varied timing of directional turnover observable across islands (25). Climate warming in the past 50 years, by contrast, is too recent to be detectable within our dataset. Over the time frame of the past 5000 years, direct human impacts greatly outweighed other processes that shaped island biodiversity and species interactions (32, 33).

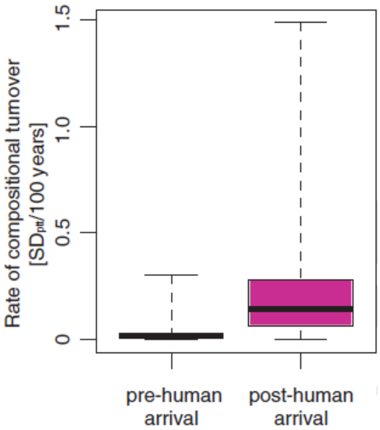

Fig. 2. Rates of turnover before and after human arrival. Change in the rate of pollen compositional turnover before (left) and after recorded date of human settlement (purple) for the time series of fossil pollen records for each of 27 islands globally, where each island's sequence has been subject to a separate ordination analysis using DCA. Rate of pollen taxon turnover is quantified as the absolute slope in the relationship between ordination scores of the first axis of each DCA with time. The units approximate standard deviation of compositional turnover per 100 years (SDptt/100 years). The pre-settlement rate of compositional turnover is represented on the left (median: 1.7×10^{-4}; mean: 4.0×10^{-4}) and the rate after human arrival is represented on the right (median: 14.7×10^{-4}; mean: 23.3×10^{-4}). The difference is highly significant ($P < 0.004$; paired *t*-test). See (*21*) for details.

Moreover, ecological legacies of human arrival on islands may persist for centuries and are often irreversible. An example is Tawhiti Rahi in the Poor Knights archipelago, which is currently uninhabited (19). Immediately after initial arrival by Polynesians in the 13th century, the island's forest cover was cleared by fire for human habitation and gardens. After a massacre of local Ngatiwai inhabitants on Tawhiti Rahi in 1820, local kaitiaki (guardians) declared the islands wahi tapu (protected by a sacred covenant), after which time there was no subsequent settlement. Despite the island becoming totally reforested within 150 years, the current forest composition is completely different from that of the pre-human period. In contrast to the Poor Knights archipelago, most currently inhabited islands have experienced at least two distinct waves of settlement, each having distinctive signatures of change and leaving increasingly complex legacies (24, 30).

Preparing and managing for ecosystem change is one of the major challenges that island societies currently face as islands experience continued or accelerated threats from detrimental land-use practices (12), new species invasions (24, 34), sea-level rise (35), and climate change (11, 17), in addition to naturally occurring disturbances. The challenges are made more difficult because these processes are affecting native ecosystems where vegetation communities have already been severely degraded or lost, species have gone extinct (15, 21), and important mutualistic plant–animal interactions have been disrupted (36). Our results show little indication that these human-affected ecosystems are either similar to or returning to the dynamic baselines observed before human arrival. Therefore, anthropogenic impacts on islands are lasting components of these systems, typically involving initial clearance (e.g., using fire), and are compounded by the introduction of a range of introduced species and extinctions of endemic species and ongoing disturbances. This contrasts with turnover after natural disturbances in the pre-human period, when island ecosystems often recovered rapidly to pre-disturbance states [e.g., (20, 31)]. Whereas for many islands, widescale return to pre-colonization ecosystems is an unrealistic goal, paleoecological data such as those analyzed here, may serve to inform targeted ecosystem restoration efforts within islands, providing insights into previous system states and their responsiveness to global change processes (9, 37).

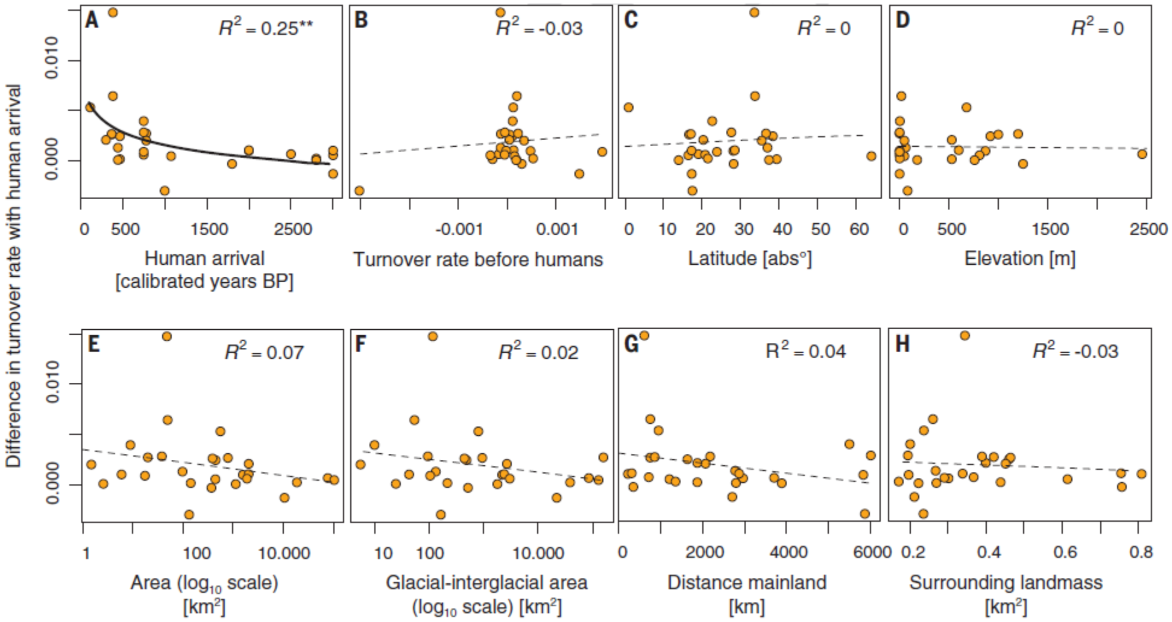

Fig. 3. Differences between the pre-human and human-dominated turnover scale with human arrival times. Relationships between the change in the rate of pollen compositional turnover before and after human arrival and several island features, showing: a curvilinear decrease in observed turnover as the time elapsed since the first colonization increases (**A**), but no relationship with turnover rate before human arrival (**B**), latitude (**C**), elevation of the coring site (**D**), island area (**E**), glacial-interglacial area (**F**), and isolation (represented by distance to mainland) (**G**), or surrounding landmass (**H**)). $^{**}P < 0.01$ (A).

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Acknowledgments: Funding: A.M.C.S was supported by a "Juan de la Cierva" Fellowship (IJCI-2014-19502) funded by the Spanish 'Ministerio de Ciencia, Innovación y Universidades', and by the Portuguese "Fundação para a Ciência e a Tecnología" (contract CEEIND/03425/2017). H.J.B.B., V.A.F., and M.J.S. were supported by the European Research Council under the EU H2020 research and innovation program Humans on Planet Earth – Long-Term Impacts on Biosphere Dynamics (HOPE grant 741413). J.P. was supported by European Research Council grant ERC-SyG-2013-610028 IMBALANCE-P. L.d.N. was supported by the European Union's Horizon 2020 research and innovation program (Marie Skłodowska-Curie 700952). M.J.S was supported by the Deutsche Forschungsgemeinschaft (STE 2360/2-1 embedded in the Research Unit TERSANE FOR 2332). S.B and K.L were supported by several grants from the Swedish Research Council (VR). S.N was supported by the Worldwide Universities Network (WUN) Research Mobility Programme and a generous sabbatical granted by the School of Geography and Environmental Science (University of Southampton). S.J.N gratefully was supported by the European Research Council under the EU H2020 and Research and Innovation program (SAPPHIRE grant 818854).

Author contributions: S.N. and M.J.S. led the study and analyzed the datasets. All authors wrote the paper and contributed to the discussion of the results.

Competing interests: The authors declare no competing interests.

Data and materials availability: Data and code are available at github.com/ManuelSteinbauer/biodiversity-changes-on-islands.

Supplementary Materials

Materials and Methods
Figs. S1 to S4
Tables S1 to S5
Citations to references (*38–109*)