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RESEARCH ARTICLE

Grassland Bird Species Decline With Colonial-Era Landscape Change in a Tropical Montane Ecosystem

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ABSTRACT

The impacts of colonial-era ecosystem changes on tropical biodiversity are poorly understood. We analyzed a 170-year dataset on land cover and bird observations in an Old World tropical montane landscape in the Western Ghats, India, to determine if and how historical landscape changes have impacted 85 bird species. A comparison of historical land cover and classified satellite imagery (1848–2018) revealed approximately an 80% decrease in grassland area and a concomitant increase in tea and timber plantations stemming from colonial-era policies and associated legacies of large-scale planting of cash crops and exotic woody species. We found that relative species abundances of about 90% of grassland birds have significantly declined while around 53% of forest bird species remained stable or even increased in relative abundance over the same period. Over 74% of generalist bird species have become more common over the same period, possibly due to reduced habitat specialization. Our findings show that colonial-era policies, continued postindependence, of tree planting across open natural ecosystems have resulted in severe loss of grassland habitats and a concomitant decline in the relative abundance of grassland bird species.

1 | Introduction

Colonial land management practices have left a lasting legacy on the patterns of biodiversity we observe today, and continue to be upheld in many parts of the world despite evidence showing that such practices are harmful to habitats, species, and ecological processes (Joshi et al. 2018; Pollini 2010). As European settlers usurped land globally, tropical landscapes were

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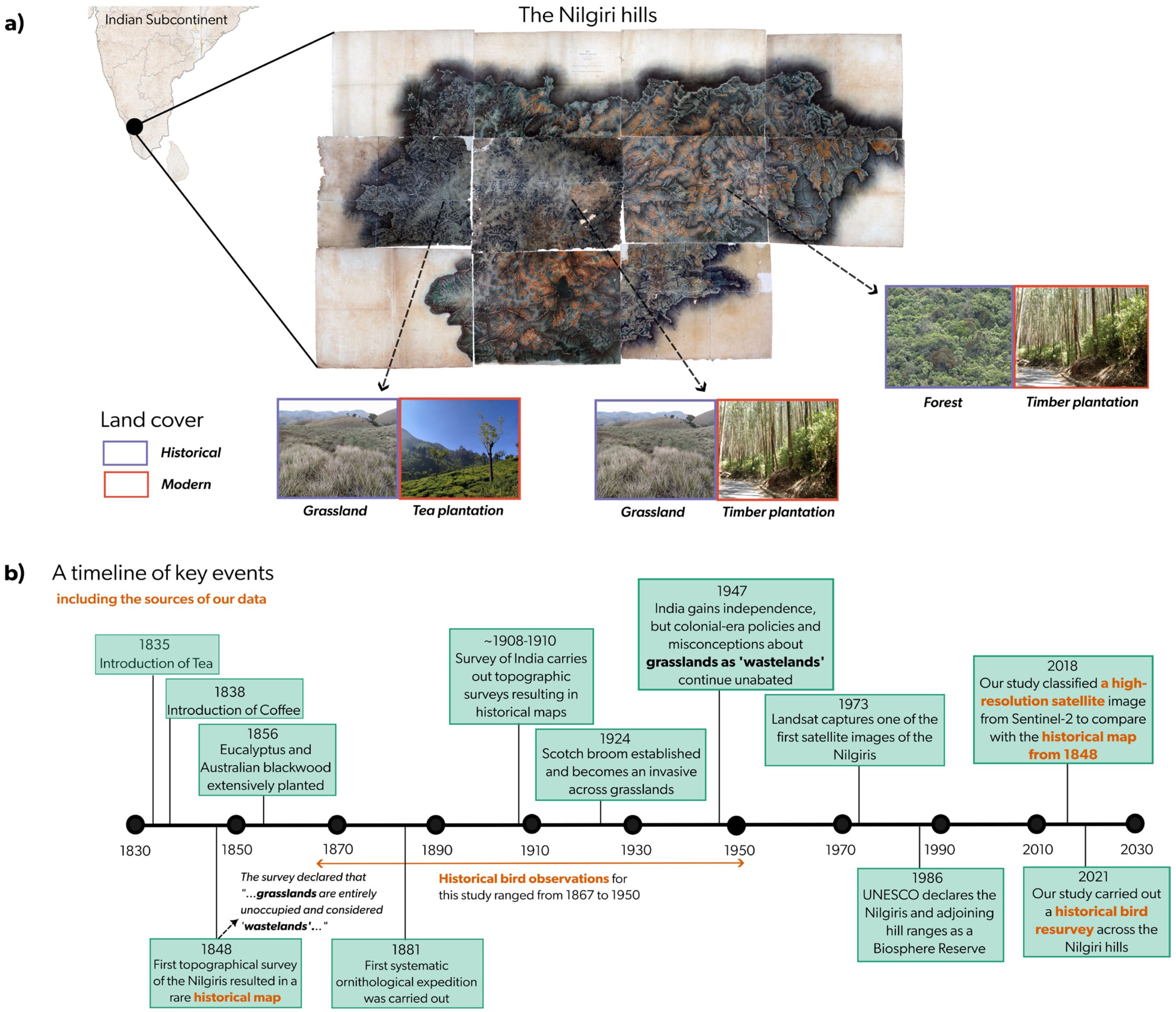

FIGURE 1 | (a) The Nilgiri hills of the Western Ghats-Sri Lanka biodiversity hotspot is the focus of our study. Shown here is the rare historical map of the Nilgiri hills, along with representative locations where land cover transitions occurred between historical (1848, colored in violet) and modern (2018, colored in red) time periods. Images of land cover were taken by Vijay Ramesh, Chandrasekar Das and Wikimedia Commons (captured by Jaseem Hamza). (b) A timeline of key events that shaped the landscape of the Nilgiri hills alongside our data sources (colored in orange) is shown here and in Table S1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

transformed for economic gain, with agricultural and timber plantations replacing forests and grasslands (Ellis et al. 2021; Pollini 2010) (Figure 1; Table S1). In particular, early colonial foresters overwhelmingly regarded grasslands as unproductive wastelands and converted vast expanses of these unique habitat types into plantations of fast-growing exotic timber species and tea (Fairhead and Leach 1996; Joshi et al. 2018; Pooley 2018). However, these land-management practices have provided us with baseline records of species abundance, land cover maps, and associated environmental data stretching back to at least two centuries.

Mountains were of particular interest to settlers, owing to the dramatic range of temperatures, vegetation, species diversity, and growing conditions that these ecosystems harbored (Grove 1997). As a consequence, they were extensively mapped worldwide, with the earliest natural history surveys providing the first systematic documentation of community assembly, species richness, and abundance (Morueta-Holme et al. 2015; von Humboldt and Bonpland 1807). In India, for example, the British created one of the first maps of the Nilgiri hills in 1822 to demarcate territories and land cover types (Price 1908). Today, by using historical biodiversity data from natural history collections along with long-term environmental data, scientists have conducted resurvey studies in several regions. Avifaunal resurveys show that while several species have been negatively impacted by warming temperatures (Forero-Medina et al. 2011; Freeman et al. 2018; Tingley et al. 2009), others are relatively resilient to environmental change (MacLean et al. 2018; MacLean and Beissinger 2017). However, a critical limiting factor that still prevents the widespread use of historical datasets to advance our understanding of bird species abundance trends is the lack of digitized environmental and species occurrence data.

We focus here on the Nilgiri hills of the Western Ghats of southern India, a tropical montane ecosystem that was colonized about 200 years ago by British settlers. Globally, tropical mountains like the Nilgiris cover less than 25% of the world's land area but support over 85% of global bird, mammal, and amphibian diversity (Rahbek et al. 2019). Throughout the tropics, long-term changes in land cover and climate are acting synergistically to cause species declines (Pollock et al. 2022), extinctions (Sekercioglu et al. 2008), and geographic range shifts (Freeman et al. 2018). In the Nilgiris, however, despite an extensive body of literature on the impacts of colonialism on human societies (Cederlöf 2005; Cederlöf and Sutton 2013; Sutton 2009), there have been no critical investigations examining the role of colonial-era landscape changes on biodiversity.

We digitized a rare, detailed historical land cover map from 1848 (Figure 1a) and compared it to satellite imagery from 2018 to quantify changes in landscape patterns. We then modeled relative species abundances of grassland (open-habitat), forest (closed-habitat), and generalist bird species (occurring in both natural and human-modified habitats) across two historical periods (1850–1900 and 1900–1950) and compared these historical bird communities to the results from a survey carried out in 2021 at the same locations. Based on observed changes in land cover, we expected that (i) grassland and forest bird species would decline in relative abundance over time while (ii) generalist birds would increase in relative abundance over time. In areas with widespread conversion of Open Natural Ecosystems (such as grasslands) to closed systems (such as timber plantations), we expected declines in the abundance of open-habitat specialists. Even if there was a net increase in the overall area covered by closed-canopy ecosystems in the landscape, we still expected closed-habitat species to decline in abundance because monoculture timber plantations likely cannot provide the necessary habitat complexity, food resources, and nesting sites for these specialists (Raman and Sukumar 2002). We expected an increase in the abundance of generalist bird species if both primary forest tracts and grassland areas declined in size in the landscape, as seen more widely across the subcontinent (SoIB 2023).

2 | Materials and Methods

2.1 | Study Area

The Nilgiri hill range is situated within the Western Ghats biodiversity hotspot of South India and is home to several endemic species of flora and fauna (Myers et al. 2000; SoIB 2023) (Figure 1). This hill range has an elevational gradient of ~2600 m and is home to a wide range of ecosystems from dry deciduous scrub forests at the lowest elevations (~300–900 m) to wet-evergreen and moist deciduous rainforests at mid-elevations (~900 m to ~1400 m) and forest-grassland mosaic ecosystems (also known as *Shola* sky islands or *Shola* forest-grassland ecosystem, which are composed of stunted evergreen forests surrounded by grasslands; *shola* is the Tamil word for a grove or forest) at the highest elevations (~1400 m to ~2600 m) (Pascal 1988).

2.2 | Landscape History of the Nilgiris

As early as the 1820s, British forces colonized the higher elevations of the Nilgiri hills (> 1400 m) and encountered a unique forest-grassland mosaic ecosystem (Jervis 1834). Prior to European colonization, the hill range was sparsely populated and home to a number of indigenous communities (Grigg 1880; Joshi et al. 2018). The upper plateau of the Nilgiri hills, due to its characteristic sky island ecosystem, reminded the colonial settlers of their native lands. In 1826, Thomas Munro, then governor of the Madras presidency, was recorded to have said "*the (Nilgiris had) numberless green knolls of every shape and size....as smooth as the lawns in an English park*" (Panter-Downes 1967). Colonial foresters believed and propagated the misconception that grasslands in the Nilgiris resulted from deforestation by indigenous and local communities through grazing and fire (Grigg 1880; Joshi et al. 2018). A narrative was established that the hill tribes had destroyed these forests over centuries due to their "ignorance and improvidence" (Joshi et al. 2018). In the 1850s, the British government began "foresting the grassland" and planted several exotic species of timber, including *Acacia*, *Pinus*, and *Eucalyptus* across the high-elevation grasslands of Nilgiri hills to meet rising demands for fuelwood (Joshi et al. 2018). Early attempts at utilizing the land for profit started with the planting of coffee (*Coffea arabica* and *Coffea canephora*), but disease and low temperatures at high elevations prevented coffee from flourishing above 1000 m. Planters switched to tea (*Camellia sinensis*), and by 1869, ~300 acres of tea were planted across the Nilgiri hills (Muthiah 1993). Today, the landscape consists of several land cover types, including exotic timber plantations, agricultural land, tea and coffee plantations, forests, grasslands, settlements, and water bodies.

2.3 | Land Cover Change Analysis

Using a combination of historical land cover maps and modern satellite imagery, we obtained a quantitative understanding of landscape change across the Nilgiri hills. Captain John Ouchterlony conducted the first systematic survey of the Nilgiri hills (largely above 1200 m in elevation) in 1848, which resulted in a detailed land cover map along with a geographical and statistical memoir (Ouchterlony 1848) (henceforth referred to as the historical map). For the historical map, we obtained scans of the respective tiles (each tile corresponds to a square grid covering a portion of the landscape) of the map from the British Library (London, United Kingdom) and the Tamil Nadu State Archive (Chennai, India). The scale is provided as 1000 feet = 1 inch and translates to a gridded spatial resolution of 6 m. Using Adobe Illustrator, the tiles of the historical map were stitched together to obtain a single image. Using QGIS (https://qgis.org/), we georeferenced the image using a series of control points obtained from an index and triangulation sheet created as part of the survey and assigned the WGS84 geographic coordinate system. Using QGIS, the historical map was then digitized by hand by AR, resulting in six land cover classes: grasslands, forests, plantations (no distinction was possible between timber and tea plantations), settlements, agricultural land, and water bodies. Historical literature and accounts were extensively relied on to ensure our classification was as accurate as possible. For instance, "unproductive wastelands" or grasslands were

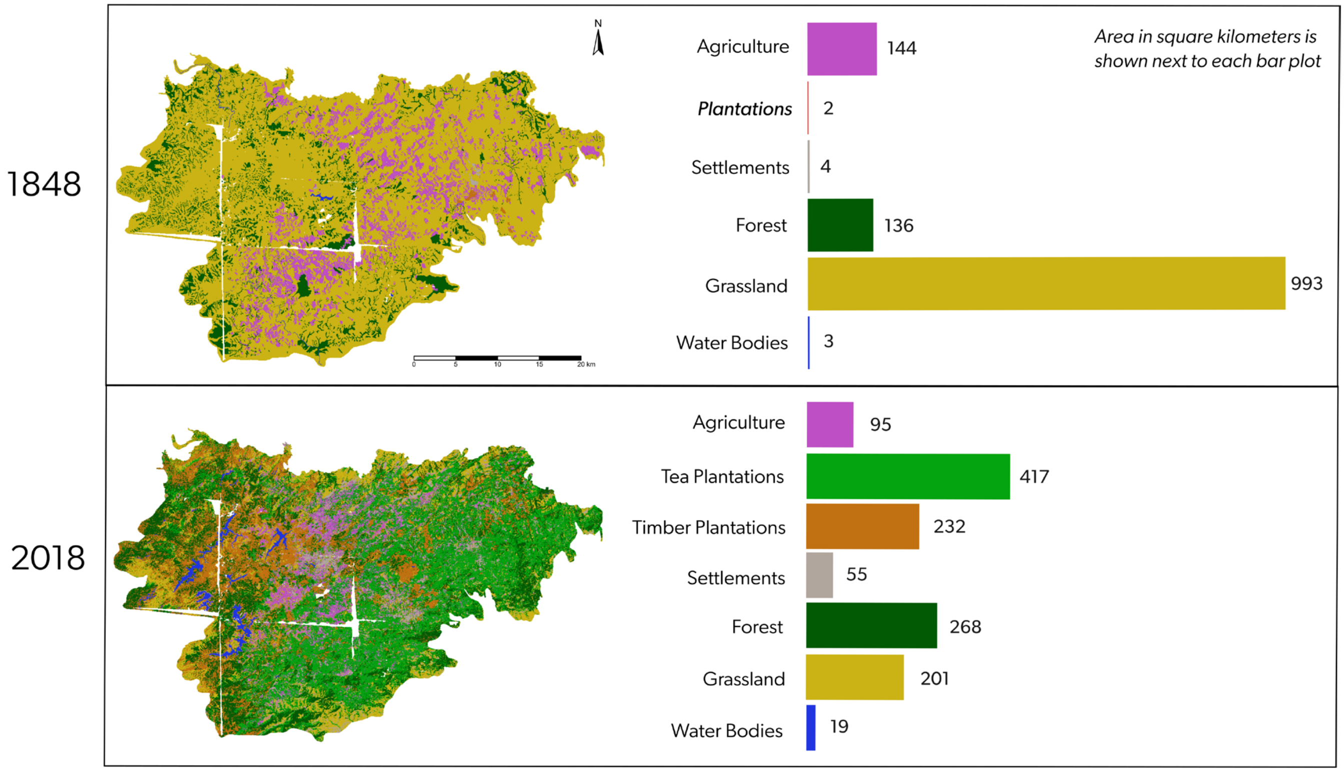

FIGURE 2 | Landscape changes over time revealed a 79.7% decrease in grassland area between 1848 and 2018. The top panel showcases the digitized version of the historical map from 1848, and the bottom panel indicates the classified satellite image from 2018. The white spaces in the map represent "NoData" areas and reflect locations that could not be digitized using the historical map. Please note that in the 1848 map, we do not have a separate land cover class for tea plantations and timber plantations as distinctions between the two were not possible. Numbers next to the bar plot represent the area of each land cover type in square kilometers.

recorded to occupy an area of 200,000 ha, and our estimate of grasslands in 1848 corresponds to 200,010 ha, which is an astonishingly minor difference.

For the modern period, we relied on satellite imagery from Sentinel-2 (spatial scale: 10 m) and accessed it using Google Earth Engine (Gorelick et al. 2017). We chose cloud-free days (< 1% cloud cover) from January 2018 to May 2018 and created a composite image. Ground truthing points were collected across the entire Nilgiris between February 2017 and March 2018 and were available from a published study (Arasumani et al. 2019). Using a RandomForests classifier ($n = 1000$ trees), we obtained a classified image with seven land cover classes (Kappa statistic = 94.1% and overall accuracy of 95.1% was achieved on the test dataset). This classified image included the same land cover classes as the historical map, aside from being able to distinguish between tea plantations and timber plantations. For more information on accessing code and analysis for the classification of modern satellite imagery, please see the Data Availability Statement.

To compare and contrast land cover and its changes over time between the historical map and the modern satellite image, we ensured that the spatial resolutions were comparable. To do so, we resampled the historical map to the same spatial resolution as the satellite image. We then created a common boundary and mask to ensure that the same areas were being compared across time periods, followed by the rasterization of each land cover class for both the historical map and the satellite image. White spaces in Figures 1a and 2 denote areas of "No Data", or locations that could not be digitized from the historical map. We then summed the total area of each land cover class by time period and compared changes over time.

Based on the results reported in Figure 2, we also carried out a supplementary analysis to validate (a) whether the majority of grassland area loss occurred during the colonial period and (b) whether forest cover has indeed increased over time. To do so, we obtained a historical Survey of India map corresponding to the years ~1908–1910 from the Library of Congress and classified satellite imagery for the years 1973 and 1995 from published literature (Arasumani et al. 2019). We carried out the change detection process, and despite our inability to digitize the entire map from ~1908 to 1910 owing to the poor quality of the map and associated changes in colors of the legend provided, we observed that the majority of grassland declines occurred in the colonial period and continued postindependence unabated (Arasumani et al. 2019; Joshi et al. 2018) (Figure S1). We also report an increase in forest cover over time, mainly in the Western Nilgiris (Figures S2 and S3).

2.4 | Climate Data

In our study, we do not report on any associations between species occurrence and climate (temperature and precipitation) as a result of poor spatial resolution of climatic data. We initially obtained daily weather data (1870–2018) from the Indian

Meteorological Department for the Nilgiri hills at a gridded resolution of 50 km × 50 km (Mishra et al. 2019). As the spatial scale at which species occurrence and land cover data were collected did not match the climate data, we refrained from carrying out analysis on testing associations between changes in temperature and precipitation and relative abundances of bird species. However, we analyzed trends in temperature and precipitation between historical and modern time periods by transforming daily weather readings (daily minimum and maximum temperature, and daily total precipitation) into mean monthly temperature and total monthly precipitation in each year. We found that while total monthly precipitation did not have a simple linear relation over time, mean monthly temperature had increased by 0.0078°C each year ($t = 50.06$; $p < 0.001$), for a mean increase of 1.03 C (SD = 0.102) during the dry season (December to May) and 1.21 C (SD = 0.0439) during the rainy season (June through November) across elevations (Figure S7).

2.5 | Historical Bird Observations

We obtained historical data on bird observations between 1850 and 1950. During this period, several natural historians, hobbyists, plantation owners, and army officers collected thousands of individual birds from across the Nilgiri hills for sport or as part of systematic surveys. We used three key sources of information to compile the historical dataset of bird species observations across the Nilgiri hills. These included historical museum specimens, published literature, and ancillary reports or diaries of collectors and ornithologists. While historical data existed between 1950 and 2000, we could not use them in our statistical analyses owing to small sample sizes.

To obtain information on historical museum specimens, we first relied on the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) to obtain digitized information on all museum specimens from the Nilgiri hills. This information included the following attributes: scientific name, locality name, date of collection (day, month, year), collector name, number of individuals, and other notes on each specimen. Several filters were used to exclude incomplete data—for example, if a preserved specimen had coarse information on the collection locality, such as "Madras" or "Nilgiris", we ignored such information. Only specimens with both years, locality names at an acceptable resolution(e.g., "Kotagiri, Nilgiris"), and species names were included in the final dataset. Second, we (VR, PRG, AVM) visited the Natural History Museum (NHM) at Tring, UK, to access data on museum specimens that are not available on GBIF or have not been digitized yet. The aforementioned attributes were obtained from each bird specimen at NHM collected from the Nilgiri hills and collated alongside data collected from GBIF.

Next, we examined published literature from 1850 to 1950 from NHM, the British Library, and online repositories like the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/). The bibliography associated with published literature is provided as Dataset S2. Only observations with attributes similar to historical museum specimens were included in the final dataset. Stringent filters were applied to published literature, and only visual sightings and mentions of preserved specimens were included; all other observations were excluded. Lastly, we collated data from diaries and notes written by collectors and natural historians from NHM. Such information included correspondences between collectors confirming how many specimens of a particular bird species were observed or collected from a specific locality in the Nilgiri hills. Our historical dataset resulted in the collation of data for 179 bird species ($n = 1626$ records) in the Nilgiri hills (Dataset S3).

2.6 | Modern Bird Resurveys

In 2021, we carried out modern bird surveys across localities from where bird species were reported during the historical time periods (1850–1950). Before carrying out resurveys, we georeferenced all historical resurvey locations with high accuracy using QGIS. For those historical localities that could not be georeferenced with high accuracy, we chose a minimum of two and a maximum of three modern survey locations within a 3 km radius around the historical locality for the modern survey. Owing to land cover changes over the last century, resurveys cannot always be carried out at the same historical location. To ensure comparability between modern surveys and historical bird observations, we used the 1848 historical map to infer the historical land cover type for the modern bird survey. A total of 42 sites were chosen for resurveys in 2021.

For example, Ooty (formerly known as Ootacamund) in the Nilgiri hills is a bustling town today and was historically a matrix of forests and grasslands. For the modern resurveys, we chose locations that corresponded to areas where forest patches occurred historically, while controlling for the 3 km radius from the historical locality (also a forest site). However, in the case of Western Catchment, a grassland site currently within a protected area, we were able to carry out a modern survey at the exact historical location. Each location was visited a minimum of two and a maximum of three times between December 2020 and June 2021. During each visit, we (VR, AA, AR, CD) carried out visual and aural observations of every bird species for a total of 15 min at each location between 0530 am and 10 am (recognized as a period of high bird activity). We followed a variable-distance point count approach and documented all bird species heard, seen, and those that flew over (primarily raptor species). Additionally, we used a single AudioMoth audio recorder (Hill et al. 2019) to simultaneously record acoustic data for the duration of the point count. Once the fieldwork was completed, the audio data was examined only to verify bird species that we could not confirm during our point count. We recorded a total of 2301 observations of 103 bird species in our modern bird surveys.

2.7 | Species Relative Abundances

Before comparing historical data with modern bird survey data, we only included species with at least three observations in the historical dataset. This filtering process resulted in 85 bird species across the 42 resurvey locations. We carried out this filtering to remove rare species or singletons. We compared historical and modern bird species data to first explore detections and non-detections of bird species across the two datasets. Here, we define detection as the recorded presence of a species and non-detection as the lack of any species record. A non-detection does not equate to an absence, as we do not possess any data on the historical effort at a site (Iknayan et al. 2014; Tingley and Beissinger 2009).

We ensured that our comparisons between the historical (1850–1900 and 1900–1950) and modern (2021) datasets were only restricted to the 85 species. As a result, several species that were reported only in the modern bird survey were excluded. We did this because even if a species was reported in the modern bird survey and not reported in the historical dataset, we cannot confirm a non-detection from our historical dataset owing to the lack of information on effort and the opportunistic nature of data collection for several species. Next, we proceeded to bin the detections and non-detections of each of the 85 bird species as a function of time period (1850–1900, 1900–1950, and 2021). The choice of these 50-year time bins—that is 1850–1900 and 1900–1950 were informed by (a) a quantitative and qualitative understanding of historical landscape changes and (b) to ensure even and sufficient sample sizes of bird species.

For each time period, we calculated the species relative abundance by applying the FAMA (Field Abundance—Museum Abundance) approach to historical data and modern survey data (Gotelli et al. 2023) (Appendix S1). To use this method, we first apply a Dirichlet distribution on the bird species counts for each time period to ensure that all species had a probability of occurrence >0, irrespective of whether it was detected in any single time period. If a species had no recorded detections at a site in a particular time period, for instance, the calculated probability of occurrence is minuscule but nonzero (Appendix S1). This analysis was run for each species at the site-level for each time period. This resulted in a value of relative abundance for each site by species by time period combination. Before inferring temporal trends and comparisons across datasets, we ran correlations between relative abundances of the historical data (pooled for 1850–1950) and the modern survey data (see (Booher et al. 2023)) to ensure that they are comparable in the first place. Our analysis revealed moderate correlations ($R^2=0.41$; with $\log_{10}$ transformation), suggesting that they are comparable even though the data was independently collected by different sources (Figure S4). All calculations were performed using the R Programming Environment (R Core Team 2023) to calculate relative abundance.

2.8 | Trait-Based Analysis

To extract data on species habitat affiliation, we relied on data from the State of India's Birds (SoIB 2023), (Ali and Ripley 1999), and historical land cover data for the Nilgiris. All 85 bird species were classified as either grassland ($n=9$), forest ($n=57$), or a generalist ($n=19$) bird species. Two reviewers vetted this classification independently to ensure that it was appropriate. We used the following reasoning to bin species into these three categories. Our historical land cover data revealed that most of the Nilgiris were largely a mosaic of forests and grasslands in 1848. Our analysis of satellite imagery in 2018 shows that the landscape today is a mosaic of several human-modified land cover types, which include timber and tea plantations, settlements, and agriculture.

While the State of India's Birds provides a habitat classification based on the contemporary use of habitat by a species, we classified species into a particular habitat affiliation based on historical land cover data. We assume that a species would either be a forest-affiliated bird species, grassland species, or a generalist species in the 1850s. An example in this case is the Black-and-orange Flycatcher (*Ficedula nigrorufa*). While it is commonly found in forest habitats, this species is also common in timber plantations today. However, the 1850s had a limited presence of timber plantations compared to 2018, and hence we assume that this is a forest specialist bird as no other wooded habitats aside from forests existed (predominantly) in the 1850s. On the other hand, if a species is truly a generalist species and is not associated with a forested or grassland habitat alone, it is classified in the generalist category.

We ran a Welch's t-test to ask if species relative abundances significantly differ between time periods (1850–1900, 1900–1950, and 2021) for grassland, forest, and generalist bird species (Figure 3). Next, we ran beta regressions to ask if species relative abundances have significantly declined or increased over time for grassland, forest, and generalist bird species. This model assumes that the response variable (relative abundance) is bounded between 0 and 1 (see (Booher et al. 2023)). Lastly, we fitted a generalized linear mixed model (estimated using maximum likelihood and nlminb optimizer) to examine if the change in grassland area over time (calculated as the difference in the proportion of grassland area within a 1-km buffer around a historical resurvey location between 1848 and 2018) is associated with the change in grassland bird species relative abundance over time (between 1850 and 1900 and 2021).

3 | Results

We report severe declines in the relative abundance of grassland birds over the last century and a concurrent loss and modification of grassland habitat across the Nilgiri hills. Land cover change analysis, using a combination of digitized historical maps and satellite imagery, revealed a 79.7% decrease in grassland area from 993 sq. km in 1848 to 201 sq. km in 2018 (Figure 2). Such decreases in grassland areas can be mostly attributed to colonial-era large-scale planting of cash crops and exotic woody species across grasslands leading to a significant increase in the area of tea and timber plantations, respectively, over time (Figure 2). Using the FAMA (field abundance—museum abundance) method (Gotelli et al. 2023) (see (2) Methods) which allows us to compare historical and modern occurrence data statistically, we found that relative abundances of grassland bird species significantly declined between historical and modern survey periods (1850–1900 vs. 2021: Beta regressions, $p=0.002$; Pseudo-$R^2=0.42$; Figure 3) with grassland specialists like the Nilgiri Pipit (*Anthus nilghiriensis*) and the Malabar Lark (*Galerida malabarica*) showing the largest decreases over time (Figure 4). On the other hand, comparisons of relative abundances of forest bird species across time periods revealed that ~53% of species ($n=30/57$; e.g., Greenish Warbler (*Phylloscopus trochiloides*), Square-tailed Bulbul (*Hypsipetes ganeesa*),

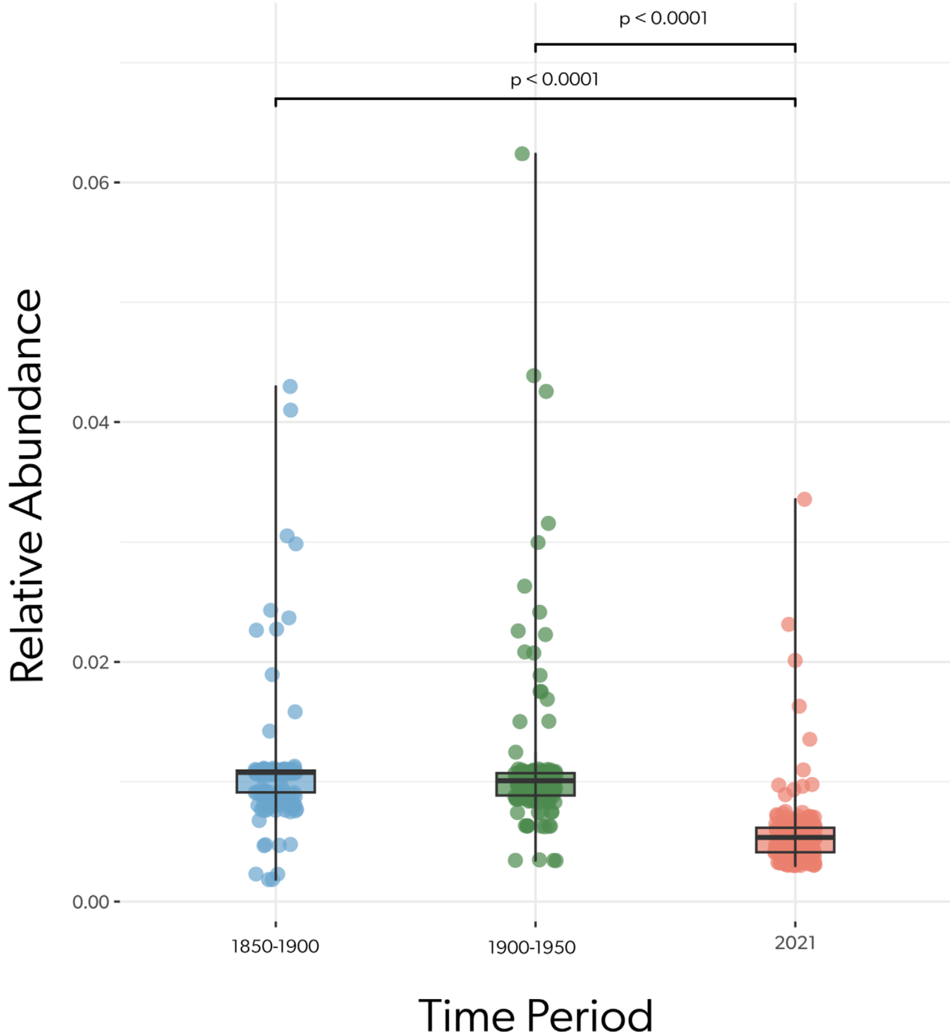

FIGURE 3 | For grassland bird species alone, Welch's t-test revealed a significant difference in relative abundances between historical and modern time periods (1850–1900 vs. 2021 and 1900–1950 vs. 2021). Each dot represents the relative abundance for a grassland species-site combination for each time period.

Crimson-backed Sunbird (*Leptocoma minima*)) showed no changes or increased in relative abundance between historical (1850–1900) and the modern resurvey (2021) data (Figure 5; Figure S5). Relative abundance comparisons for generalist species across the three time periods revealed no change or an increase by 2021 for most species (~74%; $n = 9/19$), compared to either of the two historical time periods (Figure 5; Figure S6). Among generalist species, Red-whiskered Bulbul (*Pycnonotus jocosus*) showed the greatest abundance increases from 1850 to 2021 (Dataset S1). Our linear mixed model examining whether the amount of grassland habitat loss over time was associated with the change in relative abundance of grassland birds over time revealed no statistically significant association ($p = 0.622$; Table S3).

4 | Discussion

Using historical and present-day datasets on land cover and species occurrence, we report significant declines in the relative abundance of grassland bird species. We show that this change in abundance occurs concomitantly with declines and modifications of grassland habitats that began in the colonial era (~1830).

Tropical mountains have long been regions of interest to scientists studying the effect of global change on biodiversity, and several studies have concluded that environmental change negatively impacts forest birds (Freeman et al. 2018; Ocampo-Peñuela and Pimm 2015). However, relatively little attention has been paid to grassland bird species in these regions, despite grasslands throughout the world being severely threatened and undergoing accelerated rates of degradation (Dinerstein et al. 2017; Gibbs and Salmon 2015; Lemaire et al. 2011; Veldman et al. 2015). Here, we show that in the Nilgiri hills of south India, ~90% ($n = 8/9$) of grassland species examined have declined in abundance since the first historical records were collected in the 1850s, while forest bird species have remained stable or even increased in abundance during the same time (Figure 5, Dataset S1). When we tested whether declines in grassland area were associated with declines in site-level relative abundance of grassland birds, we found no significant association indicating that: (a) grassland habitat loss has occurred uniformly across the entire landscape (Figure 2) and (b) bird abundance declines

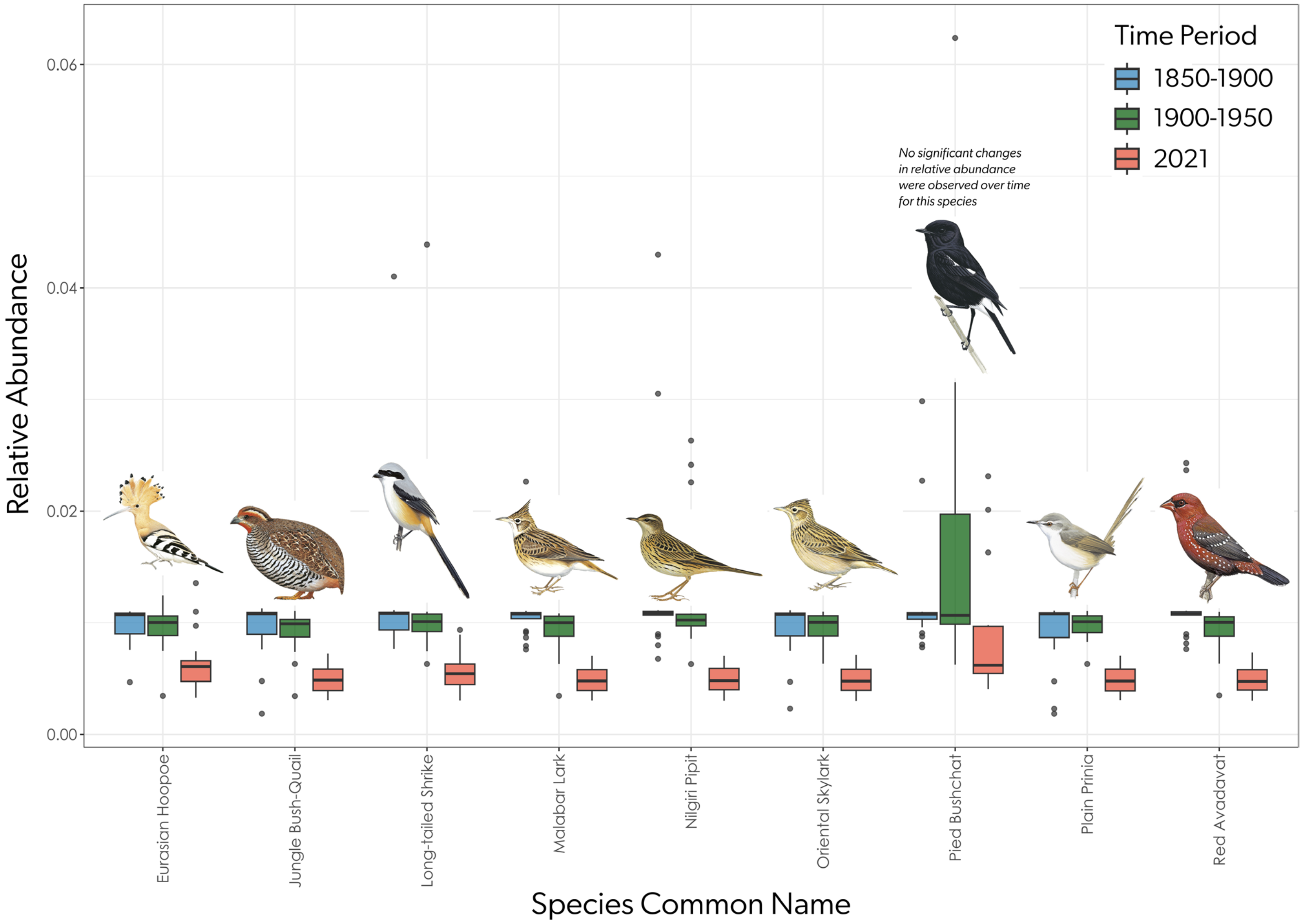

FIGURE 4 | Of the nine species of grassland birds in this study, eight species significantly declined in relative abundance over time. Only the Pied Bushchat did not show any significant changes in relative abundance across time periods. Box plots represent relative abundances for each time period (1850–1900 indicated in blue, 1900–1950 indicated in green, and 2021 indicated in red). Box plots for each species and time summarize the estimated relative abundance across all studied sites (please see (2) Methods for more details), with individual dots representing numerical outliers or extremes. Bird images were sourced from Birds of the World.

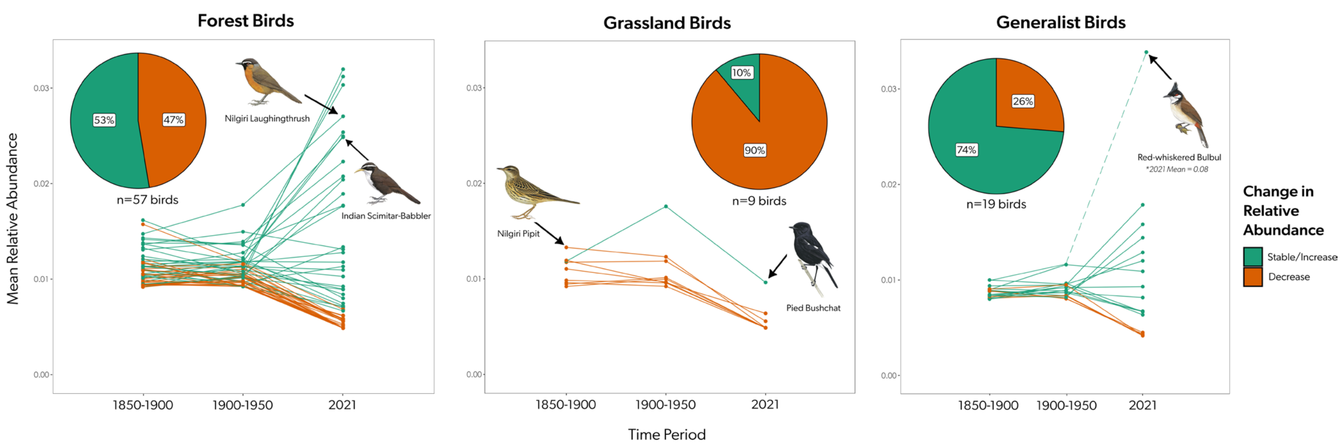

FIGURE 5 | Mean relative abundance for forest, grassland and generalist bird species is shown here for all time periods. Each dot and line represent the mean relative abundance for a given species. Lines in in green signify no change (stable) or an increase, and lines in orange signify a decrease in relative abundance in 2021 when compared to either historical time periods (see Dataset S1). Pie-charts signify the proportion of species that showed no change or increase (shown in green) and decrease (shown in orange) in mean relative abundance. The relative abundance for the Red-whiskered Bulbul is indicated with a dashed line since the mean value for this species in 2021 falls outside the limits of the y-axis here. A few representative species for each habitat affiliation is illustrated above (sourced from Birds of the World).

have also occurred uniformly. This result indicates a regional-scale process and not a local-scale process that has resulted in grassland bird declines. Despite this decline and the more obvious decline in grassland areas over the past century, only a few flagship open ecosystem-associated species, such as the Great Indian Bustard and a few vulture species across the subcontinent, have received attention from conservationists over the past several decades (SoIB 2023). Our results, however, suggest that grassland conservation and monitoring efforts will likely require a landscape-scale approach to stem further declines of grassland birds and associated taxa.

This situation is not unique to India, as grasslands and shrublands in other tropical landscapes and associated bird species continue to be ignored, and the focus is often on forest birds alone (Bengtsson et al. 2019; Overbeck et al. 2007; Sekercioglu et al. 2019; Warudkar et al. 2022). In North America, the fragmentation and loss of grasslands in the Great Plains have resulted in grassland bird populations showing the largest declines when compared to any other terrestrial biome since 1970 (Johnston et al. 2025; Lees et al. 2022; Rosenberg et al. 2019), and fire, grazing, and restoration have been suggested as methods using which to manage and conserve this habitat type (Augustine et al. 2021). Far more biodiversity-rich grassland savanna ecosystems such as the Brazilian Cerrado (Colli et al. 2020), despite being extremely rich in vascular plant diversity and undergoing conversion to agricultural land (Tingley et al. 2013), continue to receive much less conservation attention than the Amazon rainforest (Qin et al. 2022; Silveira et al. 2022). There could be two potential reasons for this deliberate valuation of forests over grasslands throughout the world. One, in India and other former European colonies (such as Madagascar and South Africa), colonial-era misconceptions about grasslands as "wastelands" have and continue to result in large-scale afforestation drives in open ecosystems (Bond et al. 2008; Joshi et al. 2018; Lahiri et al. 2023; Madhusudan and Vanak 2023; Pollini 2010; Veldman et al. 2015). The result is the fragmentation and replacement of ancient native grassland ecosystems with fast-growing plantations of timber or agricultural crops, which has cascading effects on grassland-specialist species and ecosystems (Bond 2016; Prangel et al. 2023; Sikka et al. 2003; Veldman et al. 2015). Second, grasslands are typically considered less biodiversity-rich biomes compared to tropical forests, and therefore, not high-value conservation target ecosystems. However, comparisons of biodiversity across taxonomic groups in the two biomes have shown that grasslands are only relatively species poor in terms of vascular plants and should be considered repositories of species diversity just as forests are globally (Murphy et al. 2016).

An important conclusion of our work is that around 53% of forest species, over the last 170 years of landscape change in the Nilgiris, have remained stable or even increased in relative abundance. However, during the same period, grassland specialists have severely declined and have been unable to effectively use alternative habitats to compensate for the loss of grasslands. Two mechanisms have likely shaped the persistence and resilience of forest birds and the synchronous decline in grassland-specialist abundance in this landscape: one, the planting of exotic timber plantations by the British from the 1850s to the 1930s and by the state forest department after 1947 (Arasumani et al. 2019; Joshi et al. 2018) has provided wooded habitats comparable to native forest patches which forest birds use; and two, the increase in minimum monthly temperature and global carbon dioxide concentration has promoted the colonization of grasslands by native and non-native woody species, which has significantly reduced the amount of available habitat for grassland species (Joshi et al. 2020) (Figure S7). As a result, in the Nilgiri hills, many species that are generally considered forest specialists, such as the Black-and-orange Flycatcher (*Ficedula nigrorufa*) appear to use timber plantations as extensions of native forests, similar to open-country generalists which have been shown to do the same (Hariharan and Raman 2022).

While this result somewhat contradicts other work which shows that forest specialists are more susceptible to landscape and climate change compared to open-country species (Frishkoff et al. 2016; Hendershot et al. 2020), it is important to consider the unique historical legacy of land-use change in the Nilgiri hills that has resulted in its current landscape structure. Globally, landscape change has primarily been viewed through the lens of deforestation, and forest specialists have rightly been identified as species that are negatively affected by such change (Frishkoff et al. 2014; Karp et al. 2012). However, in the Nilgiris, we show that landscape change does not simply equate to loss of wooded habitat. The context within which we argue that open ecosystem birds show more declines in abundance compared to forest birds is one in which the loss of grasslands has directly led to an increase in wooded habitat. Therefore, it is critical to establish that forest birds are more resilient than open-ecosystem birds in this particular study and context where wooded habitats have replaced grasslands and native forests. While exotic timber plantations, stands of invasive species, and degraded and logged forests act as poor substitutes for undisturbed primary forest (Edwards et al. 2011; Sheldon et al. 2010), we confirm that they are substitutes nevertheless in high-biodiversity areas. Simultaneously, it is important to note that several forest species have declined in relative abundance between 1850 and 2021, highlighting the importance of continued conservation attention in this biodiversity hotspot (Figure 5).

Generalist species, on the other hand, such as the Red-whiskered Bulbul (*Pycnonotus jocosus*) and the Large-billed Crow (*Corvus macrorhynchos*) have significantly increased in relative abundance between historical and modern survey periods (Dataset S1). Long-standing theory predicts and supports the idea that generalists, unlike specialist species, can tolerate and take advantage of a wide array of ecological niches and resource conditions (Devictor et al. 2010). In European bird communities, for example, the proportion of generalist bird species has increased in comparison to specialist birds over time (Le Viol et al. 2012). Globally, the degree to which generalists can colonize niches that forest and grassland birds occupy warrants further exploration.

Despite its limitations, our study was made possible due to extensive data collection (historical and modern sources) and integration of multiple types of data (species occurrence and land cover) across space and time. First and foremost, we acknowledge that climatic changes could have impacted changes in bird species abundances. However, we could not discern associations between changes in temperature and precipitation and avifaunal abundance, likely due to the coarse spatial and temporal resolution of historical climate data (see (2) Methods). Second, we were limited by the quality and quantity of historical data that could be used for this study, and as a result, we binned the historical species occurrence data into two time periods (1850–1900 and 1900–1950). The choice of these two time periods satisfied two criteria: (a) ensuring sufficient sample size of historical species occurrences for analysis and comparisons with modern survey data and (b) broadly capturing periods of extensive historical landscape changes (Joshi et al. 2018) (Figure 1b). We are aware that potential errors in the digitization of the historical map can bias our interpretation of land cover change over time. However, we are confident that these errors are limited, as the qualitative and quantitative estimates of the overall areas of land cover classes closely match (see (2) Methods).

In conclusion, we recommend that conservation efforts should prioritize grassland ecosystems and bird species alongside the existing protection of forests and forest birds. Unlike many forest bird species, which can take advantage of other wooded land cover types, grassland bird species in this region have been unable to take advantage of alternate habitats. Grasslands today represent one of the most threatened ecosystems globally and yet, restoration efforts have to date largely favored forests over Open Natural Ecosystems (Scholtz and Twidwell 2022). Our results emphasize that we need to prioritize Open Natural Ecosystems to preserve and protect grassland species (Staude et al. 2023) in order to effectively 'bend the curve' to stem further biodiversity loss.

Author Contributions

Vijay Ramesh: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, validation, visualization, writing – original draft, writing – review and editing. **Priyanka Hariharan:** investigation, methodology, writing – original draft, writing – review and editing. **Pratik Rajan Gupte:** data curation, formal analysis, investigation, methodology, software, writing – review and editing. **Ashwini V. Mohan:** data curation, methodology, visualization, writing – review and editing. **V. A. Akshay:** data curation, methodology, writing – review and editing. **Amrutha Rajan:** data curation, methodology, writing – review and editing. **Chandrasekar Das:** data curation. **Ian Lockwood:** data curation, formal analysis, methodology, visualization. **V. V. Robin:** conceptualization, project administration, resources, supervision, writing – review and editing. **Morgan W. Tingley:** conceptualization, methodology, project administration, software, supervision, validation, writing – review and editing. **Ruth DeFries:** conceptualization, project administration, resources, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The code and data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15831546 and https://doi.org/10.5281/zenodo.15831614 respectively. Copernicus Sentinel-2 data can be accessed at https://doi.org/10.5270/S2_-6eb6imz and via Google Earth Engine. Historical climate data can be accessed from www.imd.gov.in and via Zenodo (see above). We also include a readable version of the analyses at https://github.com/vjjan91/nilgiris-resurvey-project.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.