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Interactive impacts of climate change and land-use change on the demography of montane birds

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Abstract

Climate change and habitat degradation are amongst the two greatest threats to biodiversity. Together, they can interact to harm species. However, how climate change and land-use change jointly affect the demographic vital rates that underpin population viability remains unknown. Here, using long-term data on birds from the increasingly degraded and rapidly warming Himalayas, we show that survival trends over time are linked to species' elevational ranges in primary, but not in selectively-logged forest. In primary forest, populations at their cold-edge elevational range limit show increases in survival rates over time, while those at their warm-edge elevational range limit suffer survival declines. This pattern is consistent with species tracking favourable climatic conditions over time, leading to improved demographic outcomes at progressively higher elevations with climate change, which in turn lead to upslope range shifts. In logged forest, however, survival rates remain relatively constant over time. This suggests that in response to climate change in the long term, individuals of the same species can maintain demographic vital rates in higher-elevation primary forest, but not in logged forest. This is the first demonstration of how two of the most disruptive anthropogenic influences on biodiversity interact to threaten survivorship in natural populations. Ignoring interactions between climate change and land-use change can potentially undermine accurate forecasting of the future of species in an increasingly warm and degraded world. Importantly, large tracts of well-protected primary forests across Earth's tropical elevational gradients may be essential to enable tropical montane species to persist in the face of climate change.

Key words: apparent survival, capture-mark-recapture, elevational ranges, Himalayas, selective logging, thermal buffering, tropical mountains

Introduction

Biodiversity is increasingly in peril from two rapidly accelerating anthropogenic pressures: climate change and the conversion of natural habitats to alternative land-uses (Brook et al. 2008, Pimm 2008, Mantyka-Pringle et al. 2012). How species are affected by the interactions between these two critical threats remains largely unknown (Oliver & Morecroft 2014). Almost all empirical work has examined the biodiversity impacts of either land-use change or climate change, notwithstanding the fact that

species are exposed to, and respond to, both stressors simultaneously (Jetz et al. 2007, Frishkoff et al. 2016). Moreover, a vast majority of the studies of land-use and climate change focus on changes in species richness and abundance, or on geographical range shifts (Chen et al. 2011, Guo et al. 2018). Very few studies have examined the causal demographic mechanisms that underlie observed patterns (Ozgul et al. 2010, Wolfe et al. 2015). Those that have examined demographic mechanisms have done so for either anthropogenic land-use or climate change, but not for both. This is unfortunate because (a) climate change and land-use change do not operate independently but have combined effects on species, and (b) demographic vital rates are the ultimate determinants of species' persistence and extinction risk (Karr 1990, Korfanta et al. 2012). Understanding how these rates respond to anthropogenic pressures is imperative for effective conservation, especially because abundance-based metrics can conceal serious anthropogenic impacts on population viability (Cossett et al. 2018). However, demographic data are rarely collected in the field because doing so requires well-targeted, sustained and replicated effort over multiple years.

We used eight years of data on 4,027 captures of 2,535 individuals of 15 eastern Himalayan bird species from a study site at 2,000m ASL to examine how species' survival rates changed over time in primary versus selectively logged forest in response to both climate change and land-use change (see Methods). The Himalayas are amongst the most biodiverse terrestrial regions on Earth (Grenyer et al. 2006) and are projected to lose close to half their forest cover by 2100 (Pandit et al. 2007). Further, the Himalayan region is warming thrice as fast as the global average (Shrestha et al. 1999, Shrestha et al. 2012). Himalayan species, therefore, face significant disruptions from habitat loss and climate change combined (Pandit 2013), and they could serve as a bellwether for how biodiversity—especially in highly diverse tropical mountain ranges—may fare in an increasingly warm and degraded world.

Over our eight-year study period, we predicted that survival rates should respond rapidly to climate change for several reasons. First, tropical montane birds including eastern Himalayan species are highly temperature-sensitive (Şekercioğlu et al. 2012, Perez et al. 2016, Srinivasan et al. 2018). Second, tropical montane birds in other parts of the world have shown rapid upslope movement over the past few decades (~100m upward shifts in lower elevational range limits over 30 to 50 years [Freeman & Freeman 2014 for Papua New Guinea; Freeman et al. 2018 for Peru]); the demographic

mechanisms underlying these range shifts should be apparent at much shorter timescales than the timescales at which these range shifts occur. Third, even relatively immobile groups such as plants are showing rapid and recent distributional changes in response to climate warming in the Eastern Himalayas over relatively short timescales (seven years; Salick et al. 2019). Finally, the warming of the eastern Himalayas has accelerated greatly of late. Mean temperatures are rising swiftly, as are both the magnitude and frequency of exceptionally warm events (Krishnan et al. 2019), and the average rate of ice loss (Maurer et al. 2019). At our study site, mean summer temperatures rose by 0.02°C annually between 1980 and 2018 (Harris et al. 2014).

We predicted that, even in the absence of land-use change, across species, the direction and magnitude of survival trends over time should be related to species-specific elevational ranges. At any given elevation (here 2,000m; see Methods), some species are close to their cold-edge elevational range limit (i.e., those species with the bulk of their elevational range below 2,000m), while others are close to their warm-edge limit (i.e., those with their ranges largely above 2,000m). Still other species are close to their thermally optimal elevational range (i.e., those with the centers of their elevational ranges close to 2,000m). With warming, conditions for species near their cold-edge limit should become more thermally suitable, leading to reduced thermal stress and, in turn, resulting in increasing survivorship over time. For species at their warm-edge limit, climate warming should cause greater thermal stress and consequent survival declines. Across species, we therefore expected a negative relationship between mid-point of elevational range and survival trends (i.e., slope of survival on time), with lower-elevation species showing survival increases and higher-elevation species survival declines at 2,000m.

If selective logging and climate change do not interact, climate change should influence species' survival rates identically in both primary and logged forest (i.e., species should show similar relationships between elevational ranges and survival trends in both habitats). However, we predicted that logging and climate change would interact to affect species negatively, especially because of heightened temperature increases in anthropogenically modified forest relative to primary forest (Senior et al. 2017). Further, primary forest acts as a buffer against thermal extremes, unlike more open, anthropogenically modified, habitats (DeFrenne et al. 2019). At our site, logged forest was, on average, 2°C (95% CI = [1.91°C, 2.10°C]) warmer than primary forest (Appendix S1: Fig. S1). The

difference in maximum temperature across habitats was even more stark, with logged forest being 5.85°C [5.42°C, 6.29°C] hotter than primary forest (Appendix S1: Fig. S1). Thus, individual birds in logged forest should face greater thermal stresses than those in primary forest. We therefore expected the relationship between survival trends (i.e., slope of survival on time) and elevational range midpoint in logged forest to be even steeper than in the case of primary forest, with high elevation species at their warm-edge limits facing greater survival declines in logged than in primary forest.

Methods

Field methods

We established six plots (three each in primary and logged tropical montane broadleaved forest) centred at 2,000m ASL in Eaglenest Wildlife Sanctuary in the eastern Himalayas, Arunachal Pradesh, India (27.07°N; 92.40°E; Appendix S1: Fig. S2; Table S1). The combined area of these plots was 9 ha each in primary and logged forest. Three of these plots were either never logged or very minimally logged (< 1 tree removed ha⁻¹; tree densities [$> 10\text{cm DBH}$] of 168 to 192 trees ha⁻¹; Appendix S1: Table S1). The other three plots were intensively logged (tree densities between 76 and 110 tree ha⁻¹; Appendix S1: Table S1). Primary forest plots, therefore had roughly twice the tree density as logged plots (Appendix S1: Table S1). We chose forest patches for sampling by (a) interviewing informants involved in timber extraction-related work in the area, from whom we obtained semi-quantitative rankings of logging intensity in various forest patches, and (b) tallying rankings of logging intensity with existing vegetation structure (tree density and understorey vegetation; Srinivasan 2013, Srinivasan et al. 2015). Logging occurred until 2002, resulting in the opening of the canopy and the proliferation of bamboo in the understorey (density of bamboo stems in primary forest = $0.37\text{m}^{-2} \pm 0.07\text{SE}$; density of bamboo stems in logged forest = $0.94\text{m}^{-2} \pm 0.22\text{SE}$). The proliferation of bamboo has since slowed the recruitment of forest tree saplings in the understorey, such that vegetation structure on our sampling plots has not changed since we began sampling in 2011. Tree density and density of bamboo stems were not significantly different between 2011 and 2019 (Srinivasan, unpublished data).

Every year, from 2011 to 2018, we sampled each plot using 24-28 mist nets (12m length \times 2.4m height, 16mm mesh, 4-shelves) for three consecutive days in April-May from 0500hrs to

1200hrs (148 nets in total, each operated for 21hrs each year). April-May is the early breeding season for eastern Himalayan birds at our sampling elevation. During this period, only adults are capturable, because juveniles have not yet fledged the nest; survival estimates from capture histories therefore represent the apparent survival of adults. In each plot, we placed nets in a roughly systematic arrangement, with ~40m separating neighbouring nets (Appendix S1: Fig. S2). We checked nets every 20 to 30 minutes. Each bird captured in the nets was weighed to the nearest 0.01g using a jeweler's scale, ringed and then released immediately. Over our eight-year sampling period, only 173 (6.4 per cent) of the 2,708 individual birds were initially captured in a plot representing a particular habitat (primary or logged) and recaptured in a different habitat, indicating that sampling plots were largely independent of each other. Further, because these 173 individuals used breeding territories that included both primary and logged forest, their capture histories were excluded from the statistical analyses, yielding an analysis of the captures and recaptures of 2,535 individual birds (Appendix S1: Table S2).

Analytical methods

Estimating survival: mark-recapture analyses

We first selected species represented by at least 25 individuals each in both primary or logged forest. This yielded a total of 15 species. For each individual, we created a capture history spanning eight years (i.e., seven annual time intervals) and pooled capture histories at the species level in primary and logged forest separately. In creating capture histories, all captures within a sampling season (e.g., subsequent days) were collapsed into a single occurrence (i.e., for that sampling season, or year). We then conducted goodness-of-fit testing using the χ^2 test, to check whether the Cormack-Jolly-Seber (CJS) open population models (details below) were a good fit for each capture history (i.e., for each species in each habitat) using the “overall_CJS” function in the R Package *r2ucare* (Gimenez et al. 2018). CJS models were appropriate for the data ($0.07 < p_{\chi^2} < 0.99$; 1,728 captures of 1,082 individuals in primary forest and 2,299 captures of 1,453 individuals in logged forest; on average, ~1.6 captures per individual in each habitat; see Appendix S1: Table S2 for species-specific numbers).

We then ran capture-mark-recapture analyses for each species, separately in primary and logged forest. For each species separately in each habitat, we used Cormack-Jolly-Seber (CJS) models

to estimate apparent survival, while simultaneously accounting for imperfect detection (i.e., recapture probabilities less than 1; Cormack 1964, Jolly 1965, Seber 1965) in the package *Rmark* (Laake 2013) in program R (R Core Team 2019). Because CJS models (and open mark-recapture models in general) cannot separate mortality from permanent emigration out of the sampled area, apparent survival is a composite of true survivorship and site fidelity. We ran three models for each species in each habitat: (a) a model in which the log odds of apparent survival (ϕ) was related linearly to time, and recapture probability (p) was invariant across occasions [denoted as $\phi(T)p(.)$]; (b) a model in which the log odds of apparent survival was related linearly to time, and recapture probability varied with sampling occasion [denoted as $\phi(T)p(t)$]; and (c) a model in which the log odds of apparent survival was related linearly to time, and the log odds of recapture probability was related linearly to time. This last model was to account for the possibility that relatively long-lived tropical species that have a high familiarity with multi-year stable territories might learn to avoid mist nets over time (i.e., across years; Martin et al. 2017). A statistically significant negative coefficient relating recapture probability to time (and support from the small sample size-corrected Akaike's Information Criterion; AICc for model [c]) would indicate that individuals learned to avoid nets over the years, which might lead to negatively biased estimates of apparent survival over time.

Goodness-of-fit tests (following the decision rules outlined in Fig. 1 in Gimenez et al. 2018) also clearly showed that there was no need to account for “transient” individuals and overdispersion in the data. For each species in primary and logged forest separately, AICc was used to select the best model (Burnham & Anderson 2002), and inferences on survival increases or declines over time were made from the estimates of the best model. Because apparent survival is bound between 0 and 1, the slope relating survival to time is the log odds of survival on time. These slope values (positive for survival increases, negative for survival declines, and ~ 0 for constant survival) were used in further regression analyses.

Linear regressions

We obtained elevational range data for each species from published information on the eastern Himalayan avifauna (Spierenburg 2005), supplemented by our own data from transects spanning the elevational range at our study site (Srinivasan et al. 2018). We then calculated the mid-point of the

elevational range for each species and subtracted 2,000 (our sampling elevation) from the elevational range mid-point. Negative values, therefore, represent species with the bulk of their elevational range below our sampling location, whereas positive values indicate that the majority of a species' elevational range is above our sampling elevation. As predictors in the linear (ordinary least squares) regression, we used: (a) habitat (primary or logged), (b) the difference between 2,000 and the midpoint of species' elevational ranges, (c) body mass (log-transformed), (d) social behaviour (solitary foraging or joining mixed-species flocks), (e) migratory behaviour (elevational migrant or resident) and interactions between habitat and all species-specific traits (i.e., b—e). We selected body mass and social and migratory behaviour as predictors because prior work from the same study site indicates that these species traits might influence differential responses to selective logging (Srinivasan 2019, Srinivasan & Quader 2019). The response variable in the regression was the slope of (the log odds of) apparent survival on time. To evaluate the importance of various predictors in explaining survival trends, we used Type III sum of squares in the package *car* (Fox & Weisberg 2019) in Program R (R Core Team 2019), an approach suitable in the presence of significant interactions (Fox & Weisberg 2019). Blomberg's K from a phylogeny obtained from Jetz et al. (2012) did not indicate a phylogenetic dependence of differences in survival trends between primary and logged forest ($K = 0.94$, $p = 0.23$).

Results

We are able to analyse apparent survival trends for 15 understorey insectivorous bird species, represented by 4,027 captures of 2,535 individuals (Appendix S1: Table S2). For no species did we find evidence for permanent trap shyness (i.e., no support for model [c] based on AICc; AICc for model [c] greater than AICc for models [a] or [b] for all species in both habitats; see Methods). Further, there were no clear trends in the percentage of individuals recaptured in each year over time for any species in either primary or logged forest (Appendix S1: Fig. S3), as might be expected in the case of permanent trap shyness. Across species, initial survival rates (survival probability between 2011 and 2012) in primary forest were strongly correlated with elevational range (Pearson's $R = 0.66$ [95% CI = 0.22, 0.88]).

Over our eight-year sampling period, species showed considerable variation in survival trends in primary forest (green lines in Fig. 1; Appendix S1: Table S2). For some species, apparent survival declined over time (Fig. 1a-e), whereas others showed either constant survival over time (Fig. 1f-h) or—in most cases—increases in apparent survival (Fig. 1i-o). Most of these changes in survival over time are highly likely to be either directly or indirectly climate-driven, as there have been no changes in forest structure and composition on our primary-forest sampling plots or in the larger landscape over our study period.

The linear model explained ~45% ($R^2 = 0.44$) of the variation in survival trends over time in different habitats, of which elevational range explained the overwhelming proportion (99%; Type III R^2 [elevational range] = 0.437). Species-specific body mass and social and migratory behaviour combined accounted for a negligible amount of the variation in survival trends (Type III R^2 [mass, behaviour] = 0.07). As predicted, in primary forest, species with the bulk of their elevational ranges below 2,000m showed the greatest increases in survival over time, while species with range mid-points above 2,000m experienced survival declines ($\beta = -0.98$ [-1.6, -0.37]; Fig. 2). Species with elevational-range midpoints very close to 2,000m (our sampling elevation) showed relatively constant survival rates over time (Fig. 1e-g). These results from primary forest are consistent with climate change benefiting populations at their cold-edge limits, while harming populations at their warm-edge range limits. We expected that individuals in logged forest would be demographically disadvantaged relative to individuals in primary forest because of increased thermal stress with logging, especially for populations close to their warm-edge range limit. Contrary to our prediction, however, species-specific trends in apparent survival over time in logged forest were not related to elevational ranges ($\beta = -0.02$ [-0.21, 0.26]; Fig. 2), and most species showed no significant changes in survival over time in logged forest (Fig. 1; Appendix S1: Table S2).

Discussion

We report trends in the apparent survival of 15 bird species over an eight-year period from primary and selectively logged forest from a mid-elevation site in the eastern Himalayas. We note that apparent survival cannot separate mortality from permanent emigration; therefore, our metric represents a composite of true survivorship and site fidelity, both of which are indicative of habitat

quality (Bollinger & Gavin 1989; Knutson et al. 2016). In primary forest, as predicted, apparent survival trends were strongly correlated with species-specific elevational ranges: species close to their warm-edge elevational range limit suffered declines in apparent survival over time, whereas those at their cold-edge range limits showed increases in apparent survival (green points and line in Fig. 2). Other species traits such as size and social and migratory behaviour did not emerge as important predictors of survival trends, indicating that adaptation to the thermal environment—rather than other species traits—influences the responses of species to anthropogenic habitat change, which is supported by prior work from the Himalayan mountain range (Srinivasan et al. 2019). Given that across species, body mass was not associated with differences in survival rates in primary and logged forest, it is likely that temperature differences between primary and logged forest primarily influence fitness and survival indirectly (through, e.g., food availability) rather than through direct physiological pathways such as thermal tolerance (which are strongly tied to body size and surface area:volume ratios).

The patterns in survival we report from primary forest are consistent with the hypothesis that as temperatures rise, thermal conditions should become more favourable for populations closer to their cold-edge range limit, leading to higher survivorship and/or persistence, and therefore increases in apparent survival. In contrast, for populations already at their warm-edge range limit, rising temperatures should cause increased thermal stress, resulting in increased mortality in and/or greater emigration out of a thermally unfavourable habitat, and therefore, declines in apparent survival.

For some species (e.g., *Actinodura egertoni*, *Abroscopus schisticeps*, *Ficedula hyperythra* and *Suthora nipalensis*), steeply declining survival rates in primary forest (Fig. 1a-d) also appear to be correlated with reduced population densities in primary forest over time (Appendix S1: Fig. S4a-d). (Note that we use these raw counts of individuals in each year as indicative of trends in population density in primary and logged forest separately, because AICc-based inference does not support differences in capture probability over time in either habitat [although capture probabilities differed between habitats]; see Methods and Appendix S1: Table S2.) However, species that show increases in survival over time in primary forest (e.g., *Seicercus affinis*, *Stachyridopsis ruficeps*, *Stachyridopsis chrysaea* and *Cinclidium leucurum*; Fig. 11-o) do not necessarily also show clear increases in population densities (Appendix S1: Fig. S41-o). Overall, despite a relatively similar—or in most cases,

an even greater—number of individuals captured in logged forest than in primary forest (Appendix S1: Table S2), the annual turnover of individuals for some species in logged forest is extremely high, leading to low apparent survival. We caution that abundance-based metrics can provide misleading conclusions on habitat quality (van Horne 1983, Cossett et al. 2018) and must therefore be supplemented with demographic vital rates for accurate inference in conservation decision-making.

We note that we have not directly measured changes in temperature over time on our sampling plots, and that we cannot mechanistically demonstrate that species-specific physiological thermal optima influence climate-driven demographic trends in primary forest. Nonetheless, the eastern Himalayan region as a whole is warming rapidly (Shrestha et al. 1999, Shrestha et al. 2012), and rising temperatures can impact the survival of species directly (e.g., by increasing or mitigating thermal stress) or indirectly (e.g., through altered resource phenology and abundance or increased disease burdens). Further work is required to identify potential mechanisms and test hypotheses related to the direct and indirect effects of rising temperatures on species' demography.

Surprisingly, we did not find elevation-dependent changes in apparent survival of birds in logged forest (brown points and line in Fig. 2). We had predicted that that species-specific survival trends over time should be consistently poorer in logged forest than in primary forest. In other words, survival declines for species at the warm edge of their elevational range limits would be stronger in logged than in primary forest, and survival increases for low elevation species in primary forest would be associated with slower survival increases, no change in survival or even survival declines in logged forest. On the contrary, we found no stark changes in apparent survival over time in logged forest, unlike in primary forest (Fig. 1).

For six of 15 species (i.e., primarily low elevation species with the bulk of their elevational ranges below 2,000m ASL), apparent survival rose consistently in primary forest, but remained low (<0.60) and constant (Fig. 1k-o) or increased very slowly (Fig. 1n) in logged forest. For these species, survival trends in primary and logged forest are consistent with our predictions (see preceding paragraph). This suggests that individuals of these species can cope with climate warming by moving upslope and increasing survival rates in higher-elevation primary forest, while individuals of the same species face greater stresses if they colonize upslope logged forest, as evidenced by their inability to improve survival rates in logged forest, unlike in primary forest.

For five out of fifteen species, primarily higher elevation species with most of their ranges above 2,000m ASL, apparent survival declined over time as expected in primary forest, but contrary to our prediction, did not change significantly in logged forest (Fig. 1a-e; Appendix S1: Table S2). For these high elevation species, the patterns we report indicate that at least in the short- to medium-term, logged forest might buffer species against the survival declines they face in primary forest. For these high elevation species, however, individuals moving to higher elevations (i.e., higher than the 2,000m ASL elevation that we sample at) are likely to show increasing survival over time in high elevation primary forest and lower and constant survival in high elevation logged forest. We base this prediction on the survival patterns shown by low elevation species at 2,000 m ASL (i.e., increasing survival in primary forest, but unchanging [Fig. 1k-n] or much slower survival increases in logged forest [Fig. 1o]). In the long-term, therefore—and as temperatures increase further and entire populations of high elevation species move further upslope—it is likely that higher elevation logged forest will no longer provide a habitat that demographically buffers species against the impacts of climate change.

Further, for these species, average apparent survival in logged forest is generally low (ranging from 0.25 to 0.53), and apparent survival early on during our study (2011-2012; ranging from 0.63 to 0.88) far exceeded average survival (over eight years) in logged forest (Fig. 1a-d). (Note that initial survival between 2011 and 2012 was closely correlated with elevation [Pearson's $R = 0.66$ (0.22, 0.88)], and that for these high elevation species [Fig. 1a-e], survival in primary forest at 2,000 was strongly expected to decline over time). Further, these species (Fig. 1a-e) could be facing higher stress in logged forest, as evidenced by reductions in body mass in logged habitat (across species, mean percentage reduction in average body mass in logged forest = 9.3% [ranging from 5.0% to 22.4% across species) compared with negligible reductions in body mass for species that show survival increases in primary forest but no change in survival in primary forest (mean percentage reduction in body mass = 2.8% [0.7% to 4.8%]; Appendix S1: Fig. S5).

However, a reduction in body mass in logged forest might actually represent a response to increased ambient temperatures with logging (Appendix S1: Fig. S1). Smaller individuals can dissipate heat better, which might give them an advantage over larger individuals in significantly warmer logged forest (Appendix S1: Fig. S1). Further, if the availability of food resources is lower in

logged than in primary forest (an unexplored possibility), smaller individuals with lower absolute food requirements and consumption could be superior competitors compared with larger individuals in logged forest. Smaller size, therefore, could allow individuals to maintain survival rates in thermally stressful and/or resource-depleted anthropogenically modified habitats (Fig. 1). Nonetheless, changes in body mass with logging are likely to have implications for trade-offs in resource allocation to survival and reproduction; future research is required to understand whether maintaining survival in logged forest (potentially through reduction in body mass to deal with thermal stress; Appendix S1: Fig. S4) could come at the cost of lower fecundity (Srinivasan & Quader 2019).

On balance, therefore, tropical montane species moving upslope (Şekercioğlu et al. 2012, Freeman & Freeman 2014, Freeman et al. 2018) into degraded forest are likely to fare significantly worse than those moving upslope into primary forest. We identify potential mechanisms underlying the patterns we report. Testing these mechanisms will be important in understanding how various factors (e.g., physiological responses to thermal stress, resource availability, altered trade-offs between survival and fecundity across habitats) influence species' responses to climate- and land-use change operating jointly.

The conservation of primary forest at higher elevations is likely to be imperative to allow species to adapt to climate change by moving into thermally optimal habitats in which they can maintain survival rates. The size, distribution and spatial arrangement of primary versus logged (or otherwise degraded) forest across the elevational gradient is likely to be crucial in determining the survival of montane fauna in the face of climate change. This is especially important because maintaining survival—more than recruitment—is critical for tropical birds in preventing extinction in anthropogenically-modified habitats (Karr 1990, Korfanta et al. 2012). Crucially, although lower elevation tropical montane species may have more space to expand their ranges upward (Freeman & Freeman 2014, Freeman et al. 2018; but see Elsen & Tingley 2015), such species are unlikely to be able to deal with warming if they encounter anthropogenically degraded habitats, already widespread in the Himalayas and in other tropical montane biodiversity hotspots (Myers et al. 2000). Further, tropical species tend to be thermal specialists and temperature-constrained (Perez et al. 2016, Srinivasan et al. 2018), and should therefore respond rapidly to climate change, as our results indicate (Fig. 2). For such species, staving off extinction will likely require there to be primary forest at higher

elevations for them to occupy. Preserving viable populations of species in tropical montane biodiversity hotspots in the face of climate change thus will require large tracts of primary or old-growth forest spanning complete elevational gradients (Elsen et al. 2018).

Our results also flag crucial points for conservation inference. In recent studies of the impacts of land-use change on biodiversity (especially with respect to tropical, temperature-sensitive, species), climate effects are implicit, and almost always overlooked, even by demographic studies (e.g., Srinivasan 2019). In other words, past interactive effects between climate and land-use change can result in contemporary patterns that seem deceptively positive. For instance, in our study site, average annual survival rates of many species, averaged over the eight years of the study, did not differ significantly between primary and logged forest (e.g., Appendix S1: Fig. S31-o). One inference from this pattern might be that selective logging does not affect the demography of these species. This apparent similarity in average survival, however, masks important differences in survival trends across habitats: over the past eight years, the same species have shown increases in survival in primary forest, but not in logged forest (Fig. 11-o). In other words, these populations in logged forest are indeed severely disadvantaged in the face of climate change, a pattern that average survival estimates effectively conceal. Across species, apparent survival almost always reaches its highest values in primary forest (Fig. 1). In one species, *Ficedula hyperythra* (Snowy-browed Flycatcher), average apparent survival rates were significantly higher in primary forest than in logged forest (Appendix S1: Fig. S4c). Again, this pattern obscures important survival trends, namely, steep declines over time in survival rates in primary forest at 2,000m ASL (Fig. 1c), with possibly increasing survival in primary forest (but not logged forest) at higher elevations. Ignoring climate effects can therefore lead to misleading conclusions in predicting the impact of habitat change on species, hindering effective conservation. Long-term studies explicitly designed to tease apart the effects of climate and land-use change on vital rates are essential to adequately understand interactions between these pervasive threats to the viability of species' populations.

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Supporting Information

Additional supporting information may be found online at: [link to be added in production].

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Figure legends

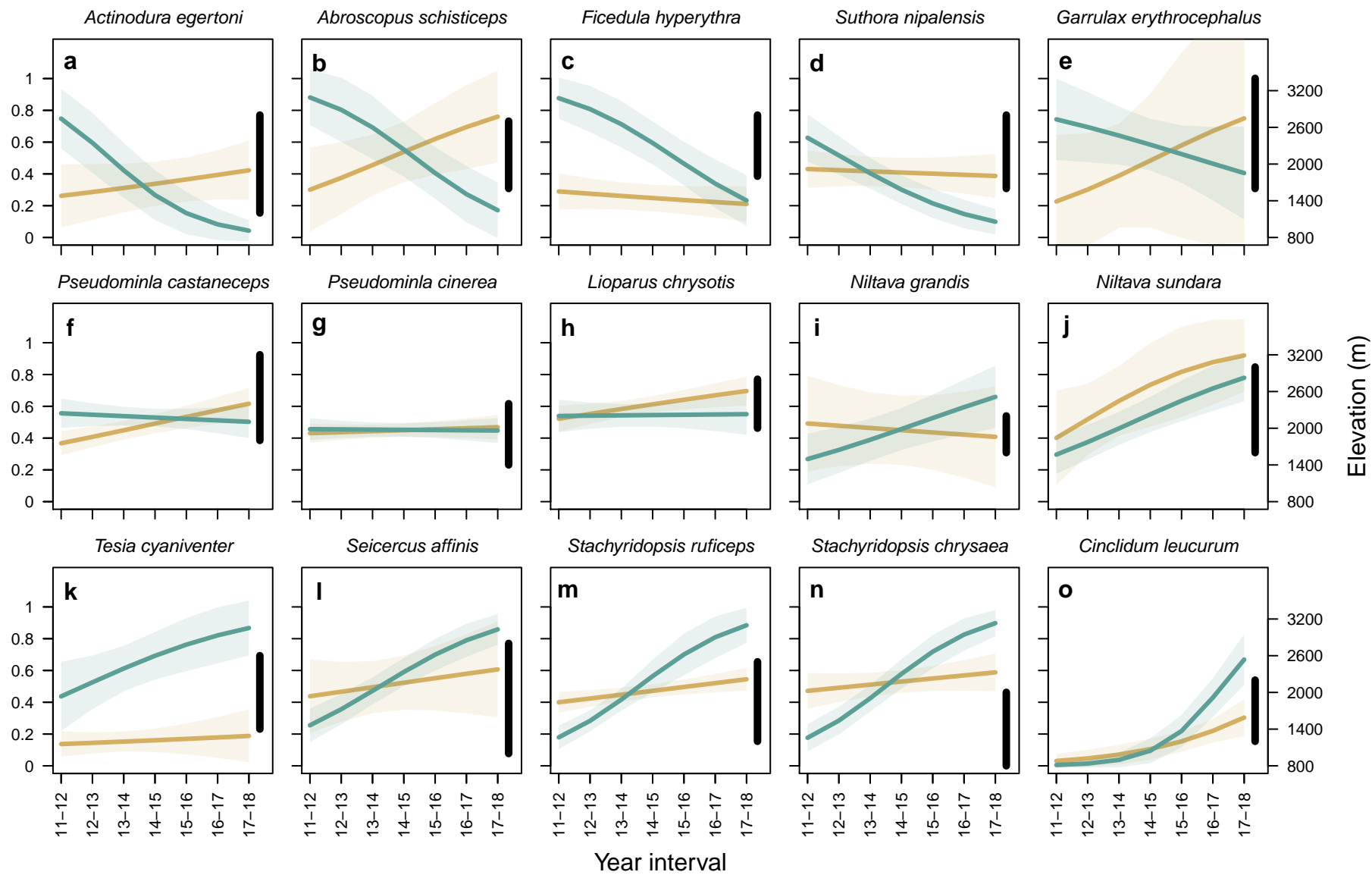
Fig. 1 | Trends in survival over time in primary and logged forest. For some species, survival declines in primary forest but increases, or remains constant, in logged forest. Others show little change in survival over time in both habitats. Yet other species show increases in survival in primary forest, but declines or no appreciable changes in survival in logged forest. Polygons around the solid lines represent one standard error of the slope. The secondary y-axis represents elevation, and the vertical black bar in every panel shows the elevational range (lower range limit to higher range limit) of each species.

Fig. 2 | Species with elevational ranges largely below our sampling elevation (negative values on the x-axis) show increasing survival over time in primary forest, while those at higher elevations (positive values on the x-axis) underwent survival declines. In contrast, survival trends in logged forest were unrelated to elevational range. Each point is a species, the solid lines are best fits from a weighted linear regression, and the polygons represent one standard error around the slopes.

Primary forest Logged forest

Apparent survival

Elevation (m)



● Primary forest ● Logged forest

