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Deforestation is the primary cause of species loss in the tropical forests that harbor much of the world's biodiversity, and understory bird species are particularly sensitive to resulting habitat fragmentation. Ongoing extinctions long after initial fragmentation suggest that demographic consequence of habitat loss are persistent, but the particular vital rates most affected and the range of demographic responses among species are not well understood. Demographic analyses can be useful in identifying the mechanisms by which fragmentation drives extinctions, assessing extinction risk for remaining populations, and guiding effective conservation planning and reserve design. Through analysis of a long-term capture-recapture dataset for understory birds of the Usambara Mountains, Tanzania, I estimated the effects of habitat fragmentation on apparent survival, recruitment, and population growth rate for 22 species in a highly fragmented sub-montane forest. I also estimated landscape-scale effects through analysis of two disjunct communities in adjacent mountain ranges. To assess the role of depressed demographic rates on the long-term persistence of the avian community on remaining forest fragments, I used count-based population viability analysis to estimate extinction risk for eight species on small (2 ha), medium (34 ha), and (704) large forest fragments. Finally, I used multi-site population viability analysis to estimate extinction risk for 14 species given four, real-world reserve scenarios. I found that across feeding guilds and dispersal abilities, apparent survival was lower on small forest fragments relative to large. Because the effect of fragmentation on recruitment was not different than zero across species, I conclude that depressed survival was the primary demographic mechanism of lower population growth rate on

small fragments. Fragmentation effects were consistent across landscapes but were more pronounced in the East Usambara Mountains relative to the West. Population viability analysis showed high extinction risk for five common species on small forest fragments and for two species on medium and large fragments. These results confirm a long faunal relaxation time and suggest continued future extinctions, particularly of less abundant species, even on the largest remaining forest fragments. Population viability analysis for four reserve scenarios showed an average delay in extinction risk of almost three decades under conditions of maximum reserve connectivity and a slight increase in protected area. Increasing dispersal among reserves was generally beneficial to population persistence, with the greatest benefit accruing through increased connectivity among the larger reserves. Many species had high extinction risk regardless of the conservation scenario, suggesting that improvements to habitat quality may also be required to maintain populations. Finally, a substantial difference in the results from demographic and species-area approaches suggests that projections of species losses from even well-protected biodiversity hotspots may be even greater than previously anticipated.

THE INFLUENCE OF HABITAT FRAGMENTATION ON DEMOGRAPHY AND
EXTINCTION RISK IN A TROPICAL UNDERSTORY BIRD COMMUNITY

by
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CHAPTER ONE

Introduction

The consequences of habitat loss and fragmentation to biological communities have traditionally been viewed through the lens of MacArthur and Wilson's (1967) classic theory of island biogeography, which postulated that lower species richness on smaller and more isolated islands results from higher extinction and lower colonization rates. Soon after it was advanced, island biogeography theory was applied to fragmented terrestrial systems, generating a rich fragmentation literature that generally supported area and isolation effects across taxa and systems (e.g., Simberloff 1976, Soulé et al. 1988, Kelt 2001, Watling and Donnelly 2006). While the predictions of island biogeography theory have proven useful for explaining or predicting broad patterns of species loss following habitat fragmentation, there is considerable variation among species in their adherence to general community-level predictions (Pimm et al. 1988, Lees and Peres 2008). Such variation arises from differences in underlying population or demographic processes that drive ultimate community-level patterns, but which are not necessarily evident from species richness or similar metrics (Lampila et al. 2005a). Also missing from an island biogeographic perspective is the ability to assess species-specific extinction risk, which can guide conservation planning and yield insights into the factors that create variation in fragmentation effects within communities (Laurance et al. 2008).

Current extinction risk theory recognizes that the sensitivity of a species to fragmentation is a function of its particular life-history attributes, as well as the traditionally considered factors of area and isolation (Reed 1999, Sekercioglu et al. 2002, Saether et al. 2005). For instance, ecological traits of individual species mediate their responses to fragment edges (Gates and Gysel 1978, Wilcove 1985), matrix (Gascon et al. 1999, Laurance 2001, Tischendorf et al.

2005), and vegetation structure. Species' responses to habitat loss and fragmentation do not occur in isolation of the broader biological community, and can be highly influenced by altered patterns of predation and meso-predator release (Crooks and Soule 1999), parasitism (Terborgh and Robinson 1986, Donovan et al. 1995), and inter- and intra-specific competition (Diamond 1972, Gilbert 1980, Feeley and Terborgh 2006). Finally, ongoing anthropogenic pressures often characteristic of fragmented landscapes – such as hunting (Peres 2001, Brashares et al. 2004, Laurance et al. 2008), altered fire regimes, and logging (Barlow et al. 2006, Michalski and Peres 2007) – may differentially influence species-specific responses. Importantly, life history and ecological correlates of extinction risk interact in complex ways and species of similar body size, longevity, feeding guild, or dispersal propensity, for example, do not necessarily respond to fragmentation in the same predictable ways (Pimm et al. 1988). As a result, the power of ecological correlates to predict extinction risk for individual species is limited (Sodhi et al. 2004).

Demographic analyses can build on insights gained from island biogeography theory and ecological correlates by identifying the underlying mechanisms that cause populations to decline or persist in fragmented environments (Lampila et al. 2005a). Population declines, and ultimately extinctions, arise from elevated mortality or emigration, depressed recruitment or immigration, or a combination of those factors. Unlike species richness and similar metrics that rely on observations of extinctions that have already occurred, demographic analyses can detect impaired populations in advance of extinction. Long-lived species, in particular, may show a long time lag between initial habitat fragmentation and ultimate population extinction (Tilman et al. 1994, O'Connell et al. 1998, Ferraz et al. 2003). For those species, vital rates may provide the most direct assessment of fragmentation impacts as well as the likelihood of population

persistence. By identifying impaired vital rates, demographic analyses can also help identify the particular ways that fragmentation influences species (e.g., depressed survival might indicate elevated predation). Finally, demographic rates and estimates of environmental stochasticity can be used to construct population viability analyses capable of estimating extinction probabilities (Morris and Doak 2002).

The research presented in this dissertation explores the demographic effects of habitat fragmentation in an understory bird community in the highly fragmented Usambara Mountains of Tanzania. Demographic analyses, and particularly those that estimate survival, typically require extensive datasets collected over a long time period. This research is possible because of the long-term capture-recapture dataset provided by Dr. William Newmark (University of Utah and the Utah Museum of Natural History), who has sampled bird populations in 14 forest fragments in the East and West Usambara Mountain ranges since 1987. Dr. Newmark's long-term study has shown that habitat fragmentation and disturbance have led to understory bird extinctions (Newmark 1991), depressed population growth rates (Newmark 2006), and altered species assemblages (Newmark 1991). This dissertation builds on these findings by identifying the likely demographic causes of altered species assemblages, determining whether depressed demographic rates persist in extant populations, and projecting future population trajectories through population viability analysis.

The Usambara Mountains, part of the Eastern Arc biodiversity hotspot, are among the most important and imperiled centers of endemism world-wide (Burgess et al. 2007b). The Eastern Arc comprises less than 0.6% of the mainland area of Tanzania but contains approximately one half of all the country's endemic plant and animal species and a majority of the globally endangered and threatened species occurring in Tanzania (Newmark 2002). The

Usambara Mountains, in particular, contain the largest number of globally threatened bird species of any of the Eastern Arc Mountains (Hipkiss et al. 1994), and several bird species have gone extinct in recent years (Newmark, unpublished data). Rapid deforestation has been driven by industrial logging, small-scale logging and firewood collection, subsistence agriculture, large-scale agriculture such as tea plantations as well as monocultures of exotic *Eucalyptus*, pine or cypress; mining; and other uses (Hall et al. 2009). With an estimated 57% deforestation in the East Usambara Mountains (EUM) and 73% deforestation in the nearby West Usambara Mountains (WUM) over the last 150 years (Newmark 2002), the area's wealth of endemism and biodiversity are maintained in a series of disconnected forest fragments.

The understory bird community of the Usambara Mountains represents an ideal study system for examining fragmentation effects. Forest remnants range in size from 0.2 – 7,806 ha, allowing for a range of intensity in fragmentation effects. Study fragments have been isolated for at least 40 years, suggesting the transient population dynamics, including short-term density increases that may immediately follow habitat loss, likely will have passed (Diamond 1972, Debinski and Holt 2000). Most understory bird species in this study are forest obligates that rarely or never use non-forested matrix habitat (Newmark 1991, Nichols et al. 1998, Borghesio et al. 2008). This means that for many species, survival and recruitment estimates were not confounded by dispersal. Most importantly, there is significant global interest in conserving and restoring biodiversity in the Usambara Mountains (Bishop and Myers 2005, Burgess et al. 2007b). Demographic analyses can identify vulnerable species and long-term population declines that might not be evident from species richness metrics (Lampila et al. 2005a). Although conservation planning must include socioeconomic, ethical, legal, and other non-biological perspectives as well (Moore et al. 2004, Chan et al. 2007), population viability

analyses can help land managers quantitatively assess the relative biological benefit of various reserve scenarios under consideration (Lindenmayer et al. 1993, Carroll et al. 2003). In this dissertation I address three primary ecological questions:

1) How does habitat fragmentation influence demography and how much variability exists

among species? In chapter two, I used mark-recapture analytical techniques to estimate apparent survival, recruitment, population growth rate, and seniority (the relative sensitivity of population growth rate to survival and recruitment) for 22 species representing a range of life-history strategies. I was able to measure the effect of fragmentation (specifically patch size) on vital rates by comparing estimates for populations on small (0.2 – 5.5 ha) and large (29.4 – 886.8 ha) forest fragments. Because study sites were distributed between adjacent mountain ranges, I also assessed the effect of landscape on vital rates – an opportunity rarely available in fragmentation studies.

2) How does extinction risk of understory bird populations vary in remaining forest

fragments? Although many tropical understory bird populations persist on small and relatively isolated forest fragments (Turner and Corlett 1999), their long-term viability is unknown. Life-history correlates provide rules of thumb for understanding relative extinction, but actual risk frequently deviates from theoretical expectations (Pimm et al. 1988, Sodhi et al. 2004). In chapter three, I constructed count-based population viability analyses for eight understory bird species to estimate relative extinction risk across species on small and large forest fragments.

3) How can demography guide reserve planning?

Reserve design is most commonly based on species richness and similar metrics, without the benefit of population persistence estimates (Cabeza and Moilanen 2001). In chapter four, I used long-term demographic data to construct a multi-site, multi-species population viability analysis with which to compare four real-world

reserve scenarios that varied in connectivity and total area protected. I used stochastic population models to estimate extinction risk based on population growth rate and environmental variance, dispersal, and spatial correlation of populations.

Chapter five is a summary and synthesis of major findings from the preceding chapters.

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CHAPTER TWO

Demographic consequences of habitat fragmentation in a tropical bird community

ABSTRACT

Tropical deforestation continues to cause population declines and local extinctions in centers of avian diversity and endemism. Although local species extinctions stem from reductions in demographic rates, little is known about how habitat fragmentation influences survival rates among bird species and ultimately shapes avian communities. We analyzed 22 years of mark-recapture data to assess how fragmentation influences apparent survival, recruitment, and realized population growth rate within 22 forest understory bird species in the Usambara Mountains, Tanzania. Long-term demographic analysis of a large suite of species experiencing the same fragmented environment revealed considerable variability in species' responses to fragmentation, in addition to general patterns that emerged from comparison among species. Across the understory bird community as a whole, we found significantly lower apparent survival and population growth rate in small fragments relative to large, demonstrating fragmentation effects to demographic rates long after habitat loss. Demographic rates were depressed across five feeding guilds and in both forest interior and forest edge specialists, suggesting even common and generalist species are sensitive to habitat fragmentation. Seniority analyses and a slightly positive effect of fragmentation on recruitment indicate that depressed apparent survival was the primary driver of population declines and observed extinctions. We also found a landscape effect, with lower vital rates in one mountain range relative to another, suggesting that fragmentation effects may add to other large-scale drivers of population decline. Overall, population growth rate (λ) estimates were < 1 in most species, suggesting that future

population persistence even within large forest fragments is uncertain in this biodiversity hotspot.

KEYWORDS

Mark-recapture, apparent survival, seniority, recruitment, understory bird, habitat loss, habitat, fragmentation, tropical biodiversity, biodiversity hotspot, Eastern Arc, Tanzania

INTRODUCTION

Past and ongoing tropical deforestation is a primary threat to avian biodiversity (Turner 1996, O'Connell et al. 1998, Gascon et al. 1999), leading to declines in species richness and shifts in community assemblages (Terborgh and Robinson 1986, Newmark 1991, Laurance et al. 2002, Sodhi et al. 2005, Ferraz et al. 2007). Underlying the local extinctions that shape avian communities are changes to the demographic processes of survival and reproduction (Lampila et al. 2005a), which vary with sensitivity to fragmentation and life-history differences among species (Sodhi et al. 2004, Lampila et al. 2005a, Lees and Peres 2006, Feeley et al. 2007). Numerical measures such as species richness metrics have revealed broad patterns of fragmentation effects on birds (Terborgh and Robinson 1986, Laurance et al. 2002, Sodhi et al. 2005, Ferraz et al. 2007) but demographic analyses that may be able to quantify fragmentation effects on population processes prior to local extinction have been less common. Likewise, demographic analysis may be preferable to population density metrics that are not always a reliable indicator of population health (Van Horne 1983, Pulliam 1988, O'Connell et al. 1998). Finally, characterizing the demographic profiles of populations on fragmented vs. continuous landscapes can isolate the most impacted demographic rates and point to the possible mechanisms likely affecting those rates (e.g., Githiru and Lens 2006).

Community-level evaluation of the effect of habitat fragmentation on tropical birds has shown broad variability in extinction risk associated with life-history differences among species (Sodhi et al. 2004, Lampila et al. 2005a, Lees and Peres 2006, Feeley et al. 2007). For instance, presence-absence studies have shown elevated extinction risk in certain feeding guilds such as insectivores (e.g., Newmark 1991, Sekercioglu et al. 2002) and among habitat specialists such as forest interior species (Bender et al. 1998). Such interspecific variability in extinction proneness suggests that underlying demographic rates should likewise vary among species and ultimately shape community-level changes following fragmentation. Yet, relatively little is known about the demographic consequences of habitat fragmentation to tropical birds (Lampila et al. 2005a). Most work has focused on boreal and temperate systems, where studies have shown generally negative effects of fragmentation on avian survival and recruitment (see Lampila et al. 2005a for a review). However, results from temperate regions may not necessarily apply to tropical systems where some bird species are longer-lived (Snow 1962, Fogden 1972, Snow and Lill 1974, Willis 1974, Faaborg and Arendt 1995, Johnston et al. 1997, Julien and Clobert 2000, Pearce-Higgins et al. 2007) and potentially more sensitive to changes in adult survival (Saether and Bakke 2000a). The few single-species studies that have examined avian survival as a function of anthropogenic habitat loss in tropical ecosystems have had mixed results (Karr 1990, Githiru and Lens 2006, Ruiz-Gutierrez et al. 2008). Further, high variation in survival among species within a single community and even among different populations of the same species (Francis et al. 1999, Sandercock et al. 2005, Blake and Loiselle 2008) may cause species to show different demographic sensitivities to environmental change, which cautions against generalizations about fragmentation effects across species. We suggest that a community-wide demographic analysis is important and needed to: 1) evaluate species-specific demographic

responses to habitat fragmentation, 2) characterize the effects of habitat fragmentation that are general to tropical avian communities, and 3) avoid bias associated with non-random selection of fragmentation-sensitive species (Lampila et al. 2005a).

In this study, we report on a long-term demographic analysis for an avian community in the Eastern Arc biodiversity hotspot (Bishop and Myers 2005). The East (EUM) and West (WUM) Usambara Mountains (Fig. 1) in northeastern Tanzania are part of the Eastern Arc chain of mountains that extend from southern Kenya to central Tanzania. Over the last 200 years, the EUM and WUM have undergone extensive deforestation, converting submontane forest to a mosaic of disjunct forest patches separated by agriculture. As a result, several understory bird species have gone locally extinct on small forest patches, creating significant species-area relationships on remaining forest fragments (Newmark 1991). Reduced nest success (Stanley and Newmark 2010) and ongoing species loss from small fragments, suggest continued demographic consequences of historical deforestation.

We used long-term (1987 – 2008) population monitoring data to determine how survival, recruitment, and population growth rate were influenced by habitat fragmentation across 22 understory bird species with varying feeding strategies, habitat requirements, and dispersal abilities. The long time span of this study is ideal for demographic analysis because vital rates are subject to short-term variation and normal periodicity, which can obscure long-term population trends if the time scale of the study is not sufficient (Wiens 1984). We used mark-recapture techniques to: 1) determine how fragmentation differentially or similarly affects demographic responses of understory bird species, 2) assess the relative sensitivities of survival and recruitment to habitat fragmentation, and 3) determine the extent to which fragmentation

effects varied at the landscape scale through sampling and analysis of populations in two geographically distinct mountain ranges (EUM and WUM).

METHODS

The EUM and WUM contain similar forest understory bird communities but are functionally distinct landscapes separated by a 17.5 km-wide, non-forested valley (Fig. 1). The elevation of study sites ranges from 972 – 1,150 m in the EUM and from 1,171 – 1,300 m in the WUM. Forests at these elevations are submontane (Iversen 1991), with mean annual rainfall totaling \approx 200 cm. Land clearing primarily for tea production and small-scale farming, has left a mosaic of remnant forest patches in the study area. Since the early 1890's, the WUM and EUM have undergone roughly 73% and 57% deforestation, respectively (Moreau 1935, Newmark 2002).

As part of a long-term study to assess forest fragmentation and disturbance effects on bird communities (Newmark 2006), we selected nine study fragments in the EUM and five in the WUM (Fig. 1). Ten fragments were 0.2 – 5.5 ha and the remaining sites were 29.4, 37.8, 521.0, and 886.8 ha. Time since fragmentation ranged from 40 – 115 years. Elevation of EUM sites ranged from 972 – 1,150 m and WUM sites ranged from 1,171 – 1,297 m. All study fragments had abrupt forest edges adjacent to cultivated tea, *Eucalyptus* plantation, or other agriculture (Fig. 1). Study sites differed in their level of disturbance, but this has not influenced detection probabilities at the species level (Newmark 2006). Time since isolation and disturbance levels varied independently of fragment size.

We used long-term capture-recapture data to estimate apparent survival, recruitment and population growth across a range of species as a function of landscape and patch size. Based on similarities in bird species assemblages in forest fragments >29 ha, we classified the two largest

fragments in both the EUM and WUM as large fragments and all others as small fragments. We considered fragment size to be a reasonable surrogate for the combined effects of edge, area, and matrix, which tended to be similar among fragments within each size class. Although it is preferable to differentiate the sometimes disparate effects of habitat fragmentation (e.g., isolation and edge effects) from habitat loss *per se* (Fahrig 2003), the Usambara Mountains are a realistically fragmented landscape in which these effects are not easily separated.

From 1987 - 2008 (22 years), we used mist nets to sample populations of understory, forest-dependent bird species. We sampled birds during the cool, dry season (June - Sept), immediately prior to the breeding season (Sept - Jan) of most species. To adequately sample larger fragments, we mist netted at multiple sites in the two largest fragments in the EUM and at the largest fragment in the WUM. We sampled most but not all sites every year; the average number of sampling years per site was 13.7 ($n = 19$, SE 1.09). Mean maximum lifespan of study species was 11.8 years ($n = 22$, SE = 0.8), more than twice as long as the longest temporal gap between surveys at any study site. We erected mist nets (12×2 m and 12.8×2 m, 36 mm mesh, four tiers) perpendicular to the edge to bisect each forest fragment, with the number of nets deployed in a fragment proportional to its area. We operated nets from dawn until dusk for three consecutive days, closing them during heavy rains and re-opening them for an equivalent duration on the fourth day. We banded captured birds (aluminum butt-end leg bands from National Band and Tag Company, model 1242), recorded standard morphometric measurements, and used plumage characteristics to sex individuals of four sexually dimorphic species including Red-faced Crimsonwing, Tambourine Dove, Forest Batis, and Eastern Double-collared Sunbird.

Twenty-two forest-dependent understory bird species from eight families, representing five feeding guilds (frugivores, nectarivores, granivores, insect gleaners/salliers, and terrestrial

insectivores), were encountered frequently enough to allow survival estimation (Table 1). With the exception of Olive Sunbird, none of these species is known to nest in any of the three main non-forested matrix types. We characterized species' willingness to disperse across non-forested matrix based on our recaptures of banded birds in different forest fragments, together with information on foraging behavior of species in *Eucalyptus* (Nichols et al. 1998) and smallholder agriculture (Borghesio et al. 2008). We characterized species as non-dispersing (no observed dispersal events during 22 years or foraging observations in matrix), low-dispersing (< 6 dispersal events and/or some records of foraging in non-forested land types), or moderate-dispersing (17 – 93 recorded dispersal events and some use of matrix habitat; Table 1).

We used open-population, Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) mark-recapture models within Program MARK (White and Burnham 1999) to test for fragmentation (large vs. small fragments) and landscape (EUM vs. WUM) effects on apparent survival (Φ_A) of each species. For the 18 non- and low-dispersing species, we expected that Φ_A , which is the product of true survival and site fidelity, closely approximated true survival. We assumed that Φ_A for the remaining species reflected some unknown amount of movement into and out of study fragments.

We performed an iterative analysis by first testing time-since-marked (TSM) and sex effects (for sexually dimorphic species), before considering models of fragmentation and landscape effects. Time-since-marked models improve accuracy by estimating survival during the year after first capture (Φ_1) separately from all later years (Φ_{2+}) (Pradel et al. 1997, Blake and Loiselle 2002, 2008, Ruiz-Gutierrez et al. 2008). For the two sexually dimorphic species with adequate sample size, we estimated Φ_A separately for females, males, and unknown-sex individuals.

For each species, we tested five models for landscape (LAND) and fragmentation (FRAG) effects including $\Phi(\cdot)$, the constant model; $\Phi_{(\text{FRAG})}$, to test for differences in survival between individuals within large vs. small fragments; $\Phi_{(\text{LAND})}$, to test for differences between the EUM and WUM landscapes; and $\Phi_{(\text{FRAG} + \text{LAND})}$, to test for additive effects. We also tested an interactive model $\Phi_{(\text{FRAG} * \text{LAND})}$ to determine whether fragmentation effects were mediated by the broader landscape context. Our sampling effort was consistent at sites sampled each year so we modeled recapture (p) as constant (or equal to 0 for missing years).

We used the median \hat{c} routine within Program MARK to estimate \hat{c} , a measure of overdispersion based on the most parameterized models, $\Phi_{(\text{TSM})}$ and $\Phi_{(\text{FRAG} * \text{LAND})}$. Because the median \hat{c} routine does not accommodate individual covariates, we estimated \hat{c} for the TSM model without sex as a covariate for sexually dimorphic species. We used \hat{c} as a variance correction factor for species with $\hat{c} > 1$ (Lebreton et al. 1992, Anderson et al. 1994). All \hat{c} estimates for survival models were less than three, indicating that the CJS model adequately modeled survival for each of the 22 species. For model selection, we used Akaike's Information Criterion (AIC_c) corrected for small sample size when $\hat{c} \leq 1$ and Quasi-AIC (QAIC_c) when model selection was corrected with $\hat{c} > 1$. For each species we used $\Delta\text{AIC} > 2$ as evidence of differences in model support, and we used likelihood ratio tests (LRT) between full and reduced models to test for effects of fragmentation and landscape ($\alpha = 0.05$). We assessed a fragmentation \times landscape interaction effect by comparing AIC support for the additive [$\Phi_{(\text{FRAG} + \text{LAND})}$] and interactive [$\Phi_{(\text{FRAG} * \text{LAND})}$] models.

We used the Pradel subroutine within Program Mark, a reverse-time capture-recapture approach, to estimate the realized population growth rate (λ) for each species (Pollock et al. 1974, Nichols et al. 1986, Pradel 1996). We tested for fragmentation and landscape effects by

modeling λ with the same five model types used in the survival analysis, including $\lambda(\cdot)$, $\lambda_{(\text{FRAG})}$, $\lambda_{(\text{LAND})}$, $\lambda_{(\text{FRAG}+\text{LAND})}$, and $\lambda_{(\text{FRAG}*\text{LAND})}$. We modeled recapture rate (p) as constant. Because data were too sparse to test a time-dependent model, we were unable to perform goodness-of-fit testing to estimate \hat{c} . We performed model selection as described for the survival analysis. We also used the Pradel subroutine in Program MARK to estimate recruitment (F) for each species, which is the addition of individuals into the population through births and immigration. We modeled F as constant, $F(\cdot)$, and as a function of fragment size, $F_{(\text{FRAG})}$, and we compared models with LRTs ($\alpha = 0.05$).

To determine the relative importance of reproduction and survival to population growth rate, we used the reverse-time approach within Program MARK to estimate the seniority parameter (γ). Seniority is a measure of the relative contribution of Φ_A to λ , while recruitment, both from reproduction and immigration, is estimated as $(1 - \gamma)$ (Nichols et al. 2000). The effect of migrants on recruitment should be low for most species in our study because inter-patch movement was rare and we omitted the few capture histories of animals that moved between fragment size classes. We estimated γ with fragmentation, $\gamma_{(\text{Frag})}$, and constant, $\gamma(\cdot)$, models.

RESULTS

We recorded > 22,000 captures of > 13,000 individuals among the 22 most commonly encountered species (Table 1). For TSM models, \hat{c} estimates ranged from 1.0 – 3.0 for 17 species, suggesting that overdispersion was not a problem. Data were slightly underdispersed ($\hat{c} < 1$) for four species (Evergreen Forest Warbler, Usambara Thrush, Sharpe's Akalat, and Spot Throat) and we did not adjust \hat{c} for these species. Little Greenbul had a relatively high \hat{c} of 4.64, suggesting overdispersion of the data or violation of assumptions of the CJS model. We used RELEASE within Program MARK to examine possible reasons for lack of model fit but found

no evidence for violations of model assumption or for systematic bias in the data. We were unable to identify an alternative model structure without information on age and sex of individuals so we simply adjusted TSM model selection by the estimated \hat{c} for Little Greenbul and interpreted results for this species cautiously. After \hat{c} adjustment, the TSM model was supported for nine species and inclusion of sex was supported for Tambourine Dove. For survival models with environmental covariates, \hat{c} estimates were very similar to those generated for TSM models and only Little Greenbul had a $\hat{c} > 3$.

Under the constant model (Φ_{TSM}), adult apparent survival (Φ_{2+}) averaged 0.735 ($n = 9$, SE 0.170) in species for which there was AIC support for the TSM model. For the remaining species, Φ calculated under the constant model ($\Phi_{(.)}$) averaged 0.650 ($n = 14$, SE 0.035). A two-sample t-test showed apparent survival estimates calculated with the TSM model were significantly greater ($t = 2.17$, $P = 0.003$) than those calculated without TSM effects, likely because the latter model included juveniles as well as adults.

Species showed variation in the degree to which survival was related to fragmentation, but most species ($n = 14$) showed lower survival rates in small fragments relative to large (Fig. 2). The constant model, Φ_{TSM} or $\Phi_{(.)}$, was best supported in 10 species, while the other models were best supported in three to five species. Likelihood ratio tests showed that Φ_A was negatively influenced by fragmentation in Olive Sunbird ($\chi_1^2 = 10.12$, $P = 0.001$), Evergreen Forest Warbler ($\chi_1^2 = 9.10$, $P = 0.003$), and White-chested Alethe ($\chi_1^2 = 10.13$, $P < 0.002$), and positively related to Φ_A in Cabanis's Greenbul ($\chi_1^2 = 5.07$, $P = 0.024$) (Fig. 2). In the 17 species for which Φ_A could be estimated in both large and small fragments, a paired t -test showed Φ_A was on average 23.8% lower in small vs. large fragments ($t_{16} = 3.14$, mean difference = 0.132; $P = 0.006$; Fig. 2).

Most species ($n = 18$) showed lower survival rates in the EUM than the WUM and five species – Olive Sunbird ($\chi_1^2 = 7.159$, $P = 0.008$), Cabanis’s Greenbul ($\chi_1^2 = 4.638$, $P = 0.031$), Tiny Greenbul ($\chi_1^2 = 4.088$, $P = 0.050$), White-chested Alethe ($\chi_1^2 = 4.088$, $P = 0.043$) and Usambara Thrush ($\chi_1^2 = 3.878$, $P = 0.049$) – had significant likelihood ratio tests for landscape effects. Across all species, survival rates were, on average, 0.064 lower in the EUM relative to the WUM, which was a significant difference ($t_{21} = -3.51$, $P = 0.002$) of 9.6% between landscapes. No species had ΔAIC support > 2 for the $\Phi_{(FRAG * LAND)}$ model relative to the $\Phi_{(FRAG + LAND)}$ model, indicating that fragmentation effects did not interact substantially with landscape.

Across species, recruitment (F) was higher in small fragments than large but the difference was not significant (paired t-test, t_{20} , mean difference = 0.102, $P = 0.115$). Two species, White-chested Alethe and Evergreen Forest Warbler, had much higher F in small fragments than large (Fig. 3) and when we removed these two species from the analysis, the fragmentation effect on recruitment was still not significantly different from zero (paired t-test, t_{15} , mean difference = 0.041, $P = 0.071$). Likelihood ratio tests showed significantly higher F in large fragments for four species: Little Greenbul ($\chi_1^2 = 14.751$, $P < 0.001$), Striped-cheeked Greenbul ($\chi_1^2 = 4.162$, $P = 0.041$), Cabanis’s Greenbul ($\chi_1^2 = 12.357$, $P < 0.001$), and Pale-breasted Illadopsis ($\chi_1^2 = -11.573$, $P = 0.001$). Six species showed significantly higher F in small fragments: Olive Sunbird ($\chi_1^2 = 7.441$, $P = 0.024$), Evergreen Forest Warbler ($\chi_1^2 = 6.048$, $P = 0.014$), Tiny Greenbul ($\chi_1^2 = -21.035$, $P < 0.001$), Yellow-throated Woodland Warbler ($\chi_1^2 = -4.007$, $P < 0.001$), White-tailed Crested Flycatcher ($\chi_1^2 = -7.125$, $P < 0.001$), and White-chested Alethe ($\chi_1^2 = 13.383$, $P < 0.001$).

Most species showed declining populations overall and more pronounced declines within small fragments. Population growth rate, estimated from the constant $\lambda(\cdot)$ model, was

significantly < 1 ($P = 0.02$) in 12 species representing each of the five guilds: Eastern Double-collared Sunbird, Evergreen Forest Warbler, Olive Sunbird, Orange Ground Thrush, Pale-breasted Illadopsis, Red-capped Forest Warbler, Red-faced Crimsonwing, Shelley's Greenbul, Spot Throat, Striped-cheeked Greenbul, Tiny Greenbul, and White-tailed Crested Flycatcher. Models with fragmentation effects [i.e., $\lambda_{(\text{FRAG})}$, $\lambda_{(\text{FRAG}+\text{LAND})}$, and $\lambda_{(\text{FRAG}*\text{LAND})}$] were best supported for eight species, and models with landscape effects were best supported in 10 species (Table 3). The constant model [$\lambda(\cdot)$] was best supported in six species (Table 3).

Population growth rate was lower (paired $t_{18} = 1.95$, $P = 0.016$) in small fragments than large (mean difference = 0.039, SE 0.015). LRTs for fragmentation effects on λ were significant in three species: Tambourine Dove ($\chi_1^2 = 3.862$, $P = 0.049$), Evergreen Forest Warbler ($\chi_1^2 = 10.171$, $P = 0.001$), and Pale-breasted Illadopsis ($\chi_1^2 = 11.573$, $P = 0.001$). Population growth rate also varied by landscape, with significantly lower λ (paired $t_{22} = -2.40$, $P = 0.025$) in the EUM than the WUM (mean difference = 0.017, SE 0.007). LRTs showed significant landscape effects in five species: Little Greenbul ($\chi_1^2 = 25.677$, $P < 0.001$), Shelley's Greenbul ($\chi_1^2 = 8.117$, $P = 0.004$), Olive Sunbird ($\chi_1^2 = 25.657$, $P < 0.001$), White-starred Forest Robin ($\chi_1^2 = 8.628$, $P = 0.003$), and Spot Throat ($\chi_1^2 = 6.022$, $P = 0.014$) (Fig. 3).

Sharpe's Akalat and White-starred Forest Robin showed significant interaction between landscape and fragmentation effects on population growth rate. For White-starred Forest Robin, the effects of fragmentation on population growth rate were reversed in the two landscapes, with higher λ within small (1.107, SE 0.025) vs. large (1.028, SE 0.029) fragments in the EUM, and higher λ in large (1.014, SE 0.017) vs. small fragments (0.965, SE 0.035) in the WUM. However, the population growth rate estimate for Sharpe's Akalat within small fragments in the

EUM had a very large error (SE 94.90) and the interaction effect appeared to be an artifact of low power to estimate that parameter.

Under the constant seniority model $\gamma(\cdot)$ survival had a greater relative effect on λ than recruitment for all species except Red-faced Crimsonwing ($\gamma = 0.340$, SE 0.075). Across all species, γ averaged 0.680 ($n = 21$, SE 0.022) and ranged from 0.340 – 0.830. For species present on both small and large fragments, γ was significantly (paired $t_{18} = 2.31$, $P = 0.033$) lower within small fragments than large (mean difference = 0.113, SE 0.049) and eight species had $\gamma < 0.5$ within small fragments, suggesting that recruitment contributed more to λ within small forest fragments than large (Fig. 3).

Although most species showed lower survival within small patches, consequences for population growth rate were mediated to varying degrees by recruitment. For instance, White-chested Alethe had the largest net difference (-0.510) in Φ_A between small and large fragments, but showed a negligible difference in λ , attributable to higher F within small fragments. Pale-breasted Illadopsis, which had the greatest difference in λ (-0.253), had a moderate reduction in Φ_A (-0.211) coupled with a large reduction in F (-0.253). Differences in Φ between small and large fragments were significantly and negatively related to differences in F (Pearson correlation = -0.67, $P = 0.003$). Across species, F was generally higher and Φ_A was lower within small fragments (Fig. 3). However, the relationship was largely driven by two species, White-chested Alethe and Evergreen Forest Warbler (Fig. 3).

DISCUSSION

Although much of the world's avian diversity exists in highly fragmented tropical forests (Turner and Corlett 1999), little is known about how habitat fragmentation affects survival (Lampila et al. 2005a). Our analysis of a large suite of understory bird species showed that local

extinctions following fragmentation are primarily due to decreased survival and that this key vital rate was depressed long after initial habitat loss. Our results confirm sensitivity of understory bird species to habitat fragmentation (Stratford and Stouffer 1999, Lees and Peres 2006) and empirically demonstrate long faunal relaxation times (Tilman et al. 1994, O'Connell et al. 1998, Ferraz et al. 2003, Metzger et al. 2009), but are novel in identifying the demographic mechanisms by which community changes result from habitat fragmentation. Most species that had a sufficient number of recaptures to test for a fragmentation effect had lower survival on small fragments. The demographic consequences of small fragment size were even more pronounced when considering that six species were no longer present within small fragments or had densities too low for survival estimation. Relatively low frequency of occurrence within small fragments created substantial error around apparent survival estimates for some species, but a pattern of lower apparent survival within small fragments was evident through a multi-species analysis, demonstrating a community-level response to forest fragmentation.

Further, we demonstrate community-wide demographic consequences of fragmentation not previously apparent from single-species studies. We found that most species in each of five feeding guilds had lower survival and population growth rate in small fragments relative to large. Our results corroborate findings from other systems that insectivorous species are particularly sensitive to forest fragmentation (Karr 1982, Canaday 1996, Stratford and Stouffer 1999, Sekercioglu et al. 2002, Ribon et al. 2003); six of the 15 insectivorous species in our study were not present within small forest fragments or were not abundant enough for survival analysis, and eight of the nine remaining species had lower survival in small fragments than large. Inability to disperse across non-forested land types was the factor most strongly associated with insectivorous bird population declines in Costa Rica (Sekercioglu et al. 2002), and limited

dispersal may exacerbate the effects of habitat loss among insectivores in this study as well. We also found depressed survival and population growth rates among nectarivores, which is surprising given that Olive Sunbird is able to use matrix habitat and because other studies in the Neotropics have found nectarivores (mostly hummingbirds) to be generally insensitive to fragment size (Stouffer and Bierragaard 1995, Lees and Peres 2006). Survival responses to fragmentation by granivores was mixed. Elsewhere, granivorous species have been shown to be more abundant within small forest fragments (e.g., Donoso et al. 2003, Lees and Peres 2006) but vagility and matrix tolerance may be more important determinants of fragmentation sensitivity than foraging style for this guild (Lees and Peres 2006). Only among frugivores was apparent survival similar in small and large fragments, consistent with work that has shown greater persistence of frugivorous birds in fragmented forested landscapes (Raman and Sukumar 2002, Lees and Peres 2006).

We also found that fragmentation effects extended beyond forest interior species to edge species, which had a consistent and negative demographic response to fragmentation. Interior species have been shown to be particularly sensitive to fragmentation (Newmark 199, but the negative effects of fragmentation should be lower for edge species that theoretically benefit from edge habitat within small fragments (Bender et al. 1998). While we confirmed generally negative effects of fragmentation on apparent survival of forest interior species (especially Usambara Thrush and Sharpe's Akalat), we also found that all edge species showed depressed survival and/or significantly declining population growth rate in small forest fragments. Thus, demographic analyses can reveal impaired population processes not necessarily evident from presence/absence studies.

By estimating both recruitment and apparent survival, we were able to evaluate the relative influence of fragmentation on these demographic rates. Although previous work has demonstrated negative effects of fragmentation on avian fecundity (Lampila et al. 2005a), we found substantial variation among species (Fig. 3), suggesting that fragmentation effects on avian recruitment are not easily generalized. Because fragmentation did not significantly depress recruitment while the effect on survival was negative across species, we conclude that depressed survival was the primary driver of population declines. Seniority analysis confirmed that survival contributed more to population growth rate than did recruitment in 21 of our 22 study species, consistent with sensitivity analyses of matrix population models for long-lived avian species (Saether and Bakke 2000a). Although the responses of survival and recruitment to fragmentation were negatively correlated, in only two species (White-chested Alethe and Cabanis's Greenbul) did recruitment increase by a level necessary to make population growth rate similar between small and large forest fragments.

A criticism of many fragmentation studies is a lack of replication at large spatial scales that could help account for the effects of landscape-scale characteristics and processes on populations (e.g., Laurance 2008). For instance, most fragmentation studies assess biotic responses to patch-level qualities (Taylor et al. 1993), yet landscape-scale qualities such as matrix composition or total habitat area might also be important in driving fragmentation responses. We found that while apparent survival and population growth rates were generally higher in the WUM than the EUM, the negative effect of fragmentation was consistent across landscapes. The landscape comparison was also useful in revealing that the fragmentation effect may be particularly detrimental to EUM populations, as evidenced by $\lambda < 1$ for many species there.

Depressed vital rates in many of the long-lived bird species we studied threatens population persistence within small fragments, as is evident from local extinctions that have already occurred (Newmark 1991). Of even greater concern is our finding that many populations had $\lambda < 1$ in large forest fragments, suggesting additional species will be lost from some of the largest remaining blocks of forest. This finding is consistent with predicted longer extinction half-lives in large forest fragments (Ferraz et al. 2003) and indicates the present amount and configuration of habitat in the EUM and WUM may not be sufficient to maintain some species over the long-term. In this and other global biodiversity hotspots, latent demographic consequences of historic landscape change are likely exacerbated by continuing habitat loss in the face of expanding human populations (Cincotta et al. 2000).

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TABLES AND FIGURES

Table 1. Scientific names, common names, and abbreviations for 22 study species. Dispersal ability was based on recapture of marked birds in different forest fragments and observations of birds in non-forested matrix (Nichols et al. 1998, Borghesio et al. 2008).

Family	Scientific name	Common name	Abbrev.	Captures/ recaptures	Dispersal
Columbidae (pigeons and doves)	<i>Turtur tymanistria</i>	Tambourine Dove	TD	193/10	Low
Timaliidae (babblers)	<i>Trichastoma rufipennis</i>	Pale-breasted Illadopsis	PBI	262/141	None
Pycnonotiidae (bulbuls)	<i>Andropadus virens</i>	Little Greenbul	LG	1,997/663	Moderate
	<i>Andropadus masukuensis</i>	Shelley's Greenbul	SG	1,651/751	Moderate
	<i>Andropadus milanjensis</i>	Striped-cheeked Greenbul	SCG	712/182	Low
	<i>Phyllastrephus placidus</i>	Cabanis's Greenbul	CG	672/507	Low
	<i>Phyllastrephus flavostriatus</i>	Yellow-streaked Greenbul	YSG	364/202	Low
	<i>Phyllastrephus debilis</i>	Tiny Greenbul	TG	446/270	Low
Turdidae (thrushes)	<i>Alethe fuelleborni</i>	White-chested Alethe	WCA	376/249	Low

	<i>Modulatrix stictigula</i>	Spot Throat	ST	130/112	None
	<i>Pogonocichla stellata</i>	White-starred Forest Robin	WSFR	211/45	Low
	<i>Sheppardia sharpei</i>	Sharpe's Akalat	SA	495/283	None
	<i>Turdus abyssinica</i>	Usambara Thrush	UT	193/113	None
	<i>Turdus gurneyi</i>	Orange Ground Thrush	OGT	224/61	Low
Sylviidae (warblers)	<i>Bradypterus barratti</i>	Evergreen Forest Warbler	EFW	208/59	Low
	<i>Orthotomus metopias</i>	Red-capped Forest Warbler	RCFW	127/22	None
	<i>Phylloscopus ruficapilla</i>	Yellow-throated Woodland Warbler	YTWW	397/119	None
Muscicapidae (flycatchers)	<i>Batis mixta</i>	Forest Batis	FB	290/57	Low
	<i>Trochocercus albonotatus</i>	White-tailed Crested Flycatcher	WTCF	503/120	Low
Nectariniidae (sunbirds)	<i>Nectarinia mediocris</i>	Eastern Double-collared Sunbird	EDCS	148/24	None
	<i>Nectarinia olivacea</i>	Olive Sunbird	OS	2,469/593	Moderate
Estrildidae (waxbills)	<i>Cryptospiza reichenovii</i>	Red-faced Crimsonwing	RFCW	646/26	Moderate

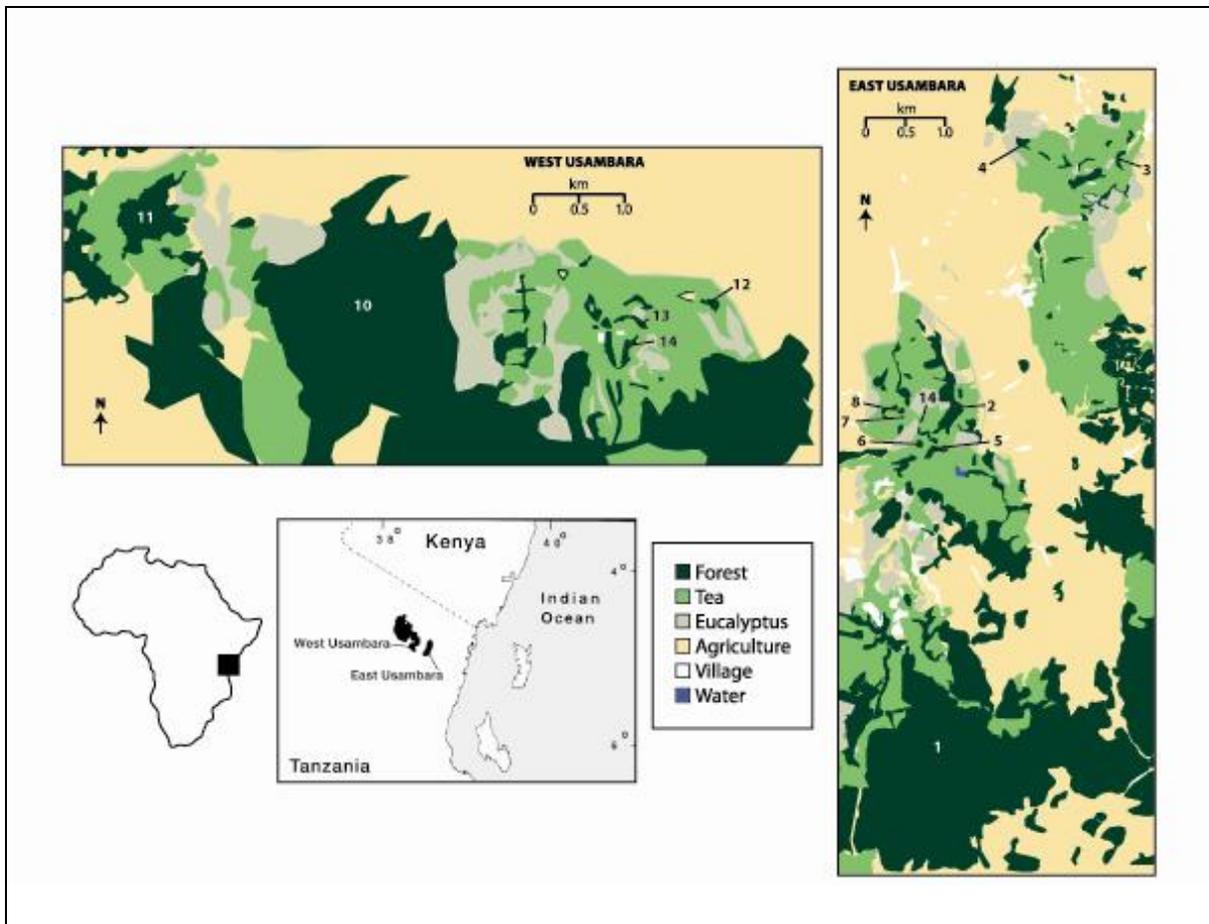


Figure 1. Land cover types and locations of study sites (1987-2008) in the East and West Usambara Mountains, Tanzania. Numbers denote study sites.

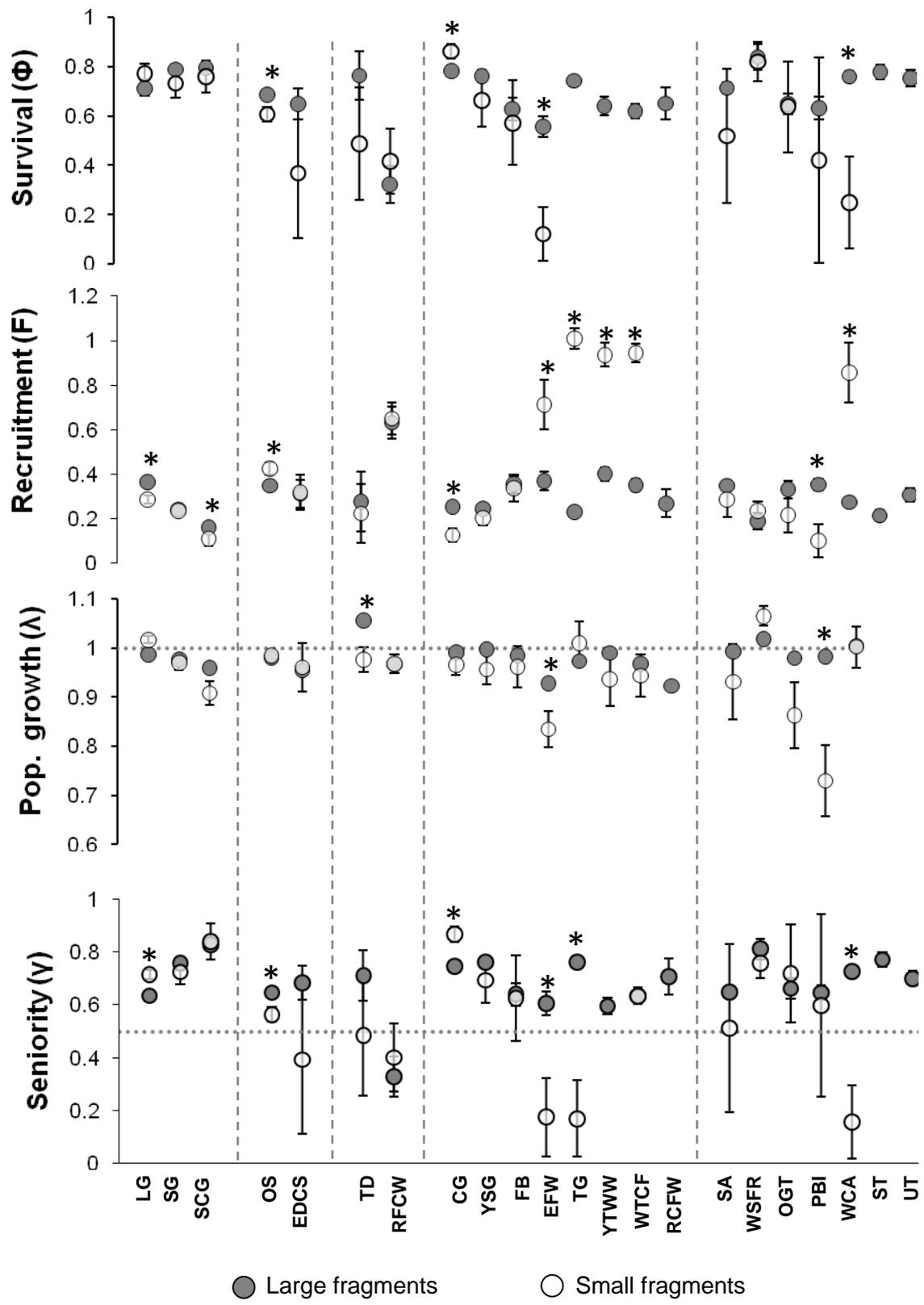


Figure 2. Apparent survival (Φ), recruitment (F), population growth rate (λ), and seniority (γ) estimates (SE) for understory bird species in large (29-887 ha) and small (0.2-5.5 ha) forest fragments in the Usambara Mountains, Tanzania, 1987-2008 (see Table 1 for species abbreviations). Asterisks denote statistically significant ($P \leq 0.05$) differences on large vs. small fragments as determined by likelihood ratio tests. Survival was not calculated for Tiny Greenbul (TG), Yellow-throated Woodland Warbler (YTWW), and White-Tailed Crested Flycatcher (WTCF) due to small sample sizes on small forest fragments. Spot Throat (ST) and Usambara Thrush (UT) are no longer detected on small forest fragments.

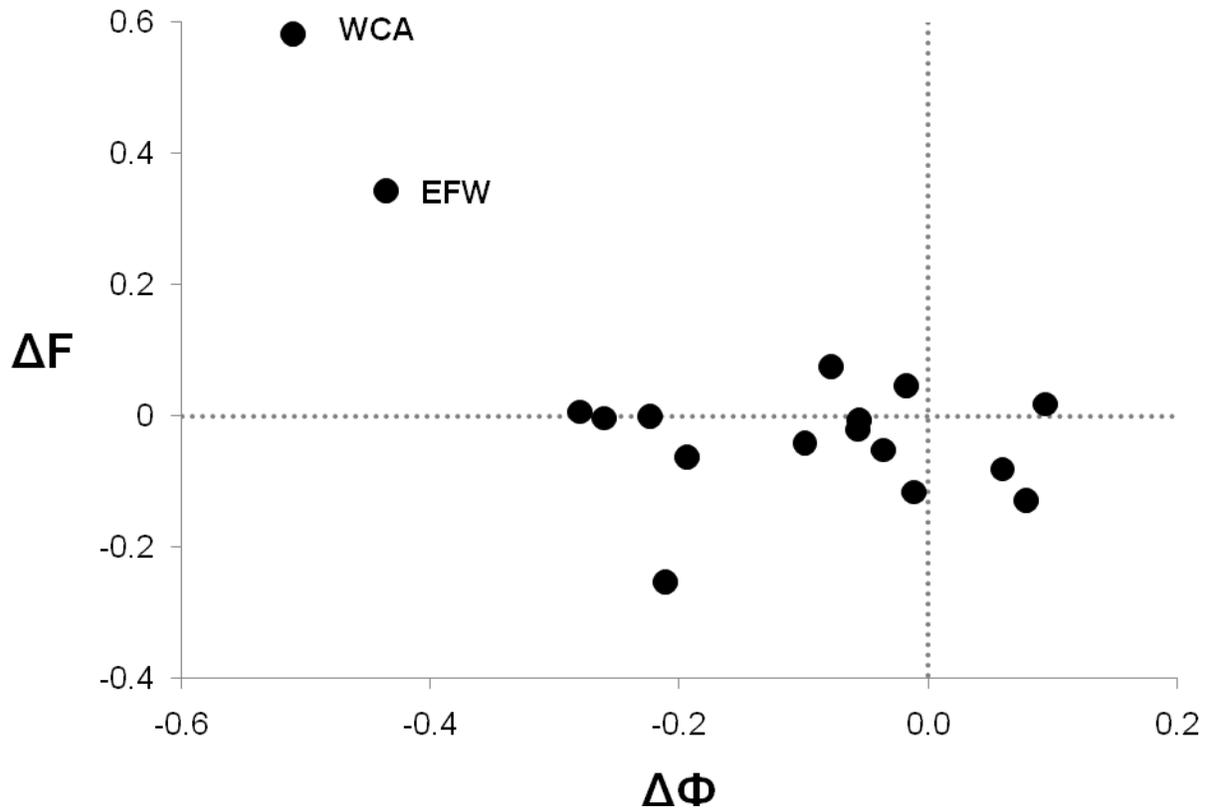


Figure 3. Relationship between changes in apparent survival (Φ) and recruitment (F) with forest fragmentation for 17 understory bird species. Each point represents the difference in apparent survival ($\Delta\Phi$) and recruitment (ΔF) between small and large forest fragments for a given species. For two species, White-chested Alethe (WCA) and Evergreen Forest Warbler (EFW), high recruitment compensated for low apparent survival on small forest fragments.

CHAPTER THREE

An empirical test of extinction risk in tropical understory birds following habitat fragmentation

ABSTRACT

A long time lag between habitat loss and ultimate species extinctions means that biodiversity will continue to decline in the fragmented tropical forests that harbor much of the world's biodiversity. The ability to identify the most extinction-prone species would help tailor conservation strategies to slow or reverse population declines, but life-history correlates typically used to assess extinction risk can have low predictive power. Alternatively, when sufficient data are available, population viability analysis can reliably estimate relative extinction risk from the population-specific demographic parameters that ultimately drive extinction risk. We used a historically-validated, count-based population viability analysis (PVA) to assess relative extinction risk of eight understory bird species on a range of forest fragment sizes in the highly fragmented Usambara Mountains, Tanzania. Based on historical patterns of extinctions, we found the PVA to be accurate for five dispersal-limited species, demonstrating that a simple count-based population model can be a powerful tool for estimating extinction risk. Species for which the PVA was not accurate were moderate dispersers for which extinction risk was overestimated, highlighting the importance of dispersal in mediating fragmentation effects. When used to estimate future risk, all species had very high extinction risk on small (2 ha) fragments, and two relatively common species had high extinction risk on medium (35 ha) and large forest fragments (704 ha) as well. Extinction risk was strongly tied to species-specific estimates of population growth rate and environmental variance, the latter of which varied with patch size. Extinction risk revealed by PVA did not, however, correlate with life-history

attributes in our small sample. Together, our results show that simply protecting remaining large forest fragments will not guarantee population persistence of the understory birds community in this biodiversity hotspot.

KEYWORDS

Population viability analysis, environmental stochasticity, population growth rate, habitat fragmentation, biodiversity, deforestation, biodiversity hotspot

INTRODUCTION

Local and range-wide species extinctions following tropical forest habitat fragmentation have been documented world-wide (O'Connell et al. 1998, Newmark 2001, Stouffer et al. 2009), but global extinctions thus far have been less numerous than previously predicted (Stork 2010). A key reason for fewer-than-expected extinctions is a long time lag between habitat loss and species loss, also known as the extinction debt (Tilman et al. 1994), that will continue to precipitate extinctions long after initial habitat loss (O'Connell et al. 1998, Ferraz et al. 2003). Although concerning for future biodiversity, the time lag between habitat loss and local or range-wide extinctions provides a window of opportunity during which we might intervene with conservation measures to slow or reverse the extinction process (O'Connell et al. 1998). To take advantage of that opportunity, however, we must understand which species are most at risk of extinction and to identify the population processes most impacted by habitat fragmentation.

Species-area curves and life-history or ecological correlates of extinction risk are the most commonly used tools to predict broad patterns of future biodiversity loss. The ubiquitous species-area curve is especially valuable for predicting final species richness following habitat loss (O'Connell et al. 1998), but the individual species most likely to drop out during faunal relaxation are not readily identified. Instead, life-history or ecological correlates of extinction

risk are used to explain differential extinction risk among groups of species based on readily observable life-history traits. For instance, larger-bodied species (Lees and Peres 2008), small populations (Newmark 1991, Pimm et al. 1993), certain feeding guilds such as terrestrial insectivores (Sekercioglu et al. 2002), and species with small range size (Harris and Pimm 2008) are all predicted to have higher extinction risk. Longevity, dispersal ability, habitat specialization, taxonomy, and other factors have also been linked to extinction risk (reviewed by Reed 1999, Henle et al. 2004, Sodhi et al. 2004, Saether et al. 2005). Life-history correlates are an important tool for understanding habitat fragmentation effects, particularly when demographic data are limited for modeling species-specific extinction risk (Lees and Peres 2008), however, their utility in predicting future extinctions is limited for two reasons. First, life-history characteristics often interact in complex and unexpected ways, making their power to predict future extinctions of individual species weak (Pimm et al. 1988, Sodhi et al. 2004). Second, life-history correlates of extinction risk are most commonly derived from post-hoc analysis of past extinction events and, as a result, are most applicable to similar, extinction-prone species. Less well understood is extinction risk of more common and less fragmentation-sensitive species that, nonetheless, may have depressed demographic rates long after initial habitat loss (Korfonta Chapter 2). As an alternative to ecological correlates, population viability analysis (PVA) has the advantage of quantifying extinction risk based on the proximate demographic factors that drive population declines, and as such, provides a more direct assessment of actual extinction risk (Lampila et al. 2005a). When data are available, multi-species PVAs are ideal for revealing the range of extinction responses within a community (Nicholson and Possingham 2006).

Much of the world's remaining tropical forests are small and isolated remnants (Turner and Corlett 1999) where the likely persistence of remaining bird populations is largely unknown.

In such places, PVA may be used to more fully develop extinction risk theory, and also to tailor conservation strategies to individual species and determine the window of opportunity for mitigation prior to local extinctions (Morris and Doak 2002, Lotts et al. 2004). When applied improperly or to insufficient datasets, PVA results may be unreliable (O'Connell et al. 1998, e.g., Coulson et al. 2001, Ellner et al. 2002, Sandercock and Beissinger 2002). Yet, when long-term demographic or count data are available to parameterize models with empirical estimates of population growth rate and its variability (Dennis et al. 1991), PVAs can reliably estimate extinction risk within and across species, as has been demonstrated in several temperate bird species of conservation concern (e.g., Donovan et al. 1995, Schleigg et al. 2005, Borkhataria et al. 2008). Particularly needed are empirically based population models that quantitatively assess individual species' risk of extinction in the tropical biodiversity hotspots that harbor exceptional endemism but are threatened by extensive habitat loss (Bishop and Myers 2005, Laurance 2007). Nevertheless, to our knowledge, PVA has not been applied to avian communities in tropical biodiversity hotspots or other fragmented tropical forests, where long-term data are typically limited, but the need for viability analyses is great.

The Eastern Arc Mountains, including the East (EUM) and West Usambara Mountains (WUM) in northeast Tanzania, is a biodiversity hotspot that has undergone extensive deforestation and now comprises a series of mostly isolated forest fragments in a matrix of agricultural and other land uses (Hall et al. 2009). As a result, some understory bird species have gone locally extinct and assemblages on remaining forest fragments show a strong species-area relationship (Newmark 1991). Even 40 – 115 years after fragmentation, remaining populations continue to show depressed demographic rates (Korfanta Chapter 2). For instance, apparent survival was significantly lower on small forest fragments relative to large across a suite of 22

species, leading to significant population declines for many populations of these long-lived species. Future population trajectories are, however, determined not only by population growth rate (λ), but also by demographic and environmental stochasticity that cause variation around λ (Lande 1993). A key advantage of PVA is the ability to estimate population persistence as a function of both deterministic and stochastic processes (Sandercock and Beissinger 2002). Although future extinctions in this biodiversity hotspot seem likely (O'Connell et al. 1998), species-specific extinction risk has not been quantified.

Based on 22 years of mist netting data, we constructed modified count-based PVAs for eight understory bird species in the Eastern Arc to estimate relative extinction risk across species and forest fragment sizes. The eight species represented a range of life-history attributes and fragmentation responses in terms of persistence on remaining forest fragments (Newmark 2001, Newmark 2006) and demography (Korfanta Chapter 2). Our long-term study design provided two key opportunities that are rarely available when estimating extinction risk for species of concern. First, we parameterized our models with estimates of population growth rate and variation drawn from a long time period, which is a key requirement of constructing reliable PVAs (Coulson et al. 2001). Second, we were able to validate the predictive power of the PVAs using observed patterns of species loss in the study area. Because local extinctions have occurred during the sampling period, and can presumably account for species missing from forest fragments prior to the study, we were able to test PVAs against historical patterns of extinction to validate them prior to estimating future extinction risk (O'Connell et al. 1998). The objectives of our study were to: 1) assess the relative sensitivities of understory bird species to forest fragmentation and compare them to predictions of extinction risk from ecological correlates, 2) determine whether forest fragment sizes typical of remaining habitat in fragmented tropical

forests are sufficient to sustain avian populations into the future, and 3) quantify species-specific patch size requirements to refine land management and conservation goals.

METHODS

Field methods

The EUM and WUM, which are separated by the 17.5 km-wide, non-forested Lwengera Valley, have undergone roughly 73% and 57% deforestation, respectively, over the last two centuries (Moreau 1935, Newmark 2002). The once-continuous submontane forest is now present mostly as remnants of forest fragments in a matrix of tea and eucalyptus (*Eucalyptus globulosus* and other species) plantations, villages, and small farms (Fig. 1). For more than two decades, we (WDN) have been monitoring the understory bird community in remnant forest patches to assess the effects of forest fragmentation and disturbance on persistence and demography (Newmark 1991, 2006). Annually, from 1987 to 2009, we have studied understory bird populations in nine forest fragments in the EUM and five in the WUM. Fragment sizes in the EUM were 0.2 (2), 0.6, 0.8, 2.2, 2.6, 3.3, 29.4, and 521.0 ha. Fragment sizes in the WUM were 1.5, 1.9, 5.5, 37.8, and 886.8 ha.

Each year since 1987, we sampled understory forest birds during the cool, dry season (June - Sept), immediately prior to the breeding season (Sept - Jan) of most species. To sample larger fragments adequately, we mist netted at multiple sites in the two largest fragments in the EUM and at the largest fragment in the WUM. We sampled most, but not all, sites annually, with an average number of sampling years per site of 13.7 ($n = 19$, SE 1.09). We banded captured birds with aluminum butt-end leg bands from National Band and Tag Company (model 1242) and used plumage characteristics to sex birds when possible. For additional details on the study site and mist net sampling design, see Korfanta Chapter 2. In recent years, we have

expanded on this work to include spot mapping in the EUM to estimate population densities for PVA model parameterization. During a single breeding season at sites within the two largest forest fragments, we mapped the estimated locations of singing and sighted birds as a perpendicular distance to the nearest trail marker located at 25 m intervals within a 50 m grid and estimated average individuals/100 ha based on the resulting territory map.

We focused our evaluation of species-specific extinction rates on eight species with varying population growth rate estimates in small (0.2 – 5.5 ha) and large (29.0 – 887.0 ha) forest fragments (Table 1). We selected the study species based on data resolution and because they represented a range of fragmentation responses and feeding guilds (Table 1). Of the 49 total species captured, the study species were among the 11 most commonly captured species, with the exception of Tambourine Dove (*Turtur tymanistris*), which was 20th. The eight species also varied in their abilities to disperse among patches. In 22 years of mist netting, we recaptured very few individuals (< 6) of Tambourine Dove, Striped-cheeked Greenbul (*Andropadus milanjensis*), Yellow-streaked Greenbul (*Phyllastrephus flavostriatus*), or White-chested Alethe (*Alethe fuelleborni*) in study fragments other than where they were initially captured, suggesting limited dispersal by these species. Moderate dispersers included Red-faced Crimsonwing (*Cryptospiza reichenovii*), Shelly's Greenbul (*Andropadus masukuensis*), and Olive Sunbird (*Nectarinia olivacea*), each of which had between 17 and 34 dispersal events to nearby study fragments. We defined Little Greenbul (*Andropadus virens*) as a relatively good disperser, with 96 recaptures of individuals on different forest fragments. The species also varied in body size, ranging from 9.3 g for Olive Sunbird, to 68.3 g for Tambourine Dove (see Newmark 1991 for more detail).

Population viability analysis

For each species, we estimated extinction risk using count-based PVA, which models population persistence from estimates of population growth rate and its environmental variation, along with estimates of population size (Dennis et al. 1991, Lande 1993, Morris and Doak 2002). We used a modification of a count-based PVA (Dennis et al. 1991) based on estimates of population growth rate (λ) derived from mark-recapture analysis rather than through annual population counts.

We used Pradel's lambda routine, a reverse-time, capture-recapture technique (Pollock et al. 1974, Nichols et al. 1986, Pradel 1996) within Program MARK (White and Burnham 1999), to estimate realized λ for populations on small and large forest fragments from the full 22 years of data. Previous work has shown that patterns of local avian extinction in the EUM and WUM differed between fragments of two size classes: large fragments, > 20 ha, and small fragments, ranging from 0.2 to 5.5 ha (Korfanta Chapter 2). Pradel's lambda routine estimates λ by also modeling recapture rate (p) and apparent survival (Φ). Because our sampling effort was consistent among sites visited within a year and between years, we modeled recapture rate as constant, and set $p = 0$ in years that a site was not sampled. To estimate Φ , we used best-fit models from a previous analysis (Korfanta Chapter 2) designed to test the effects of time since marking (TSM) to deal with effect of transients (Pradel 1996), sex (SEX; for sexually dimorphic species), fragmentation (FRAG; large versus small fragment size), landscape (LAND; East versus West Usambara Mountains), and the interaction between these two factors. Final models used to estimate λ on small and large forest fragments for each species were: Tambourine Dove – $p(\cdot)\Phi_{(\text{SEX})} \lambda_{(\text{FRAG})}$; Little Greenbul - $p(\cdot)\Phi_{(\text{TSM}+\text{FRAG})} \lambda_{(\text{FRAG})}$; Shelly's Greenbul $p(\cdot)\Phi_{(\text{TSM})} \lambda_{(\text{FRAG})}$; Striped-cheeked Greenbul - $p(\cdot)\Phi(\cdot)\lambda_{(\text{FRAG})}$; Yellow-streaked Greenbul $p(\cdot)\Phi(\cdot)\lambda_{(\text{FRAG})}$; White-

chedsted Alethe - $p(\cdot)\Phi_{(TSM+LAND+FRAG)}\lambda_{(FRAG)}$; Olive Sunbird - $p(\cdot)\Phi_{(TSM+LAND+FRAG)}\lambda_{(FRAG)}$; and Red-faced Crimsonwing - $p(\cdot)\Phi(\cdot)\lambda_{(FRAG)}$, where constant models are denoted by (\cdot) and additive models are denoted by $(+)$. We converted λ to μ using the relationship from the log-normal distribution:

$$\mu \cong \ln\bar{\lambda} - \frac{1}{2} \ln \left[\left(\frac{var\bar{\lambda}}{\bar{\lambda}^2} \right) + 1 \right].$$

Temporal estimates of population growth rate contain two sources of variation: 1) temporal or environmental variation, which represents actual process variation in population size through time, and 2) sampling variation, which arises from imperfect population counts and should be accounted for when possible (Link and Nichols 1994). Within Program MARK, we estimated process variance as described by White et al. (2002) to isolate temporal variance (σ^2) in time-dependent models that estimated λ annually. Because we were unable to produce reasonable estimates of λ for missing sample years when using the entire 22-year, we estimated σ^2 from the nine years of λ estimates (1992-2000) for which we had annual sampling records across all sites. We transformed the environmental variance estimate (σ^2) from Program MARK to a geometric approximation ($\sigma_{\frac{\mu}{\lambda}}^2$) with the relationship:

$$\sigma_{\frac{\mu}{\lambda}}^2 \cong \ln \left[\left(\frac{var\bar{\lambda}}{\bar{\lambda}^2} \right) + 1 \right].$$

Other parameters required by the diffusion approximation method include the time horizon for the analysis (years), the starting or current population size (N_c), and the quasi-extinction threshold (N_e), or the size at which the population is effectively extinct. We estimated N_c by multiplying species' population density estimates from spot mapping, by the size of each forest fragment (Table 1). Larger forest fragments with more complete species assemblages may

have lower population densities of individual species (MacArthur et al. 1972, McGrady-Steed and Morin 2000, Stevens and Willig 2000, Wethered and Lawes 2003). As such, our estimates of N_c might be biased low and potentially overestimate extinction risk on small forest fragments. On the other hand, some understory bird species expand their home ranges on small forest fragments and, as a result, have lower population densities (Hansbauer et al. 2008). To determine how bias in N_c might affect estimates of extinction risk on small fragments, we doubled our N_c estimate for each species and compared the probability of quasi-extinction with that produced by an uncorrected N_c . We found the differences to be $\ll 1\%$ so we assumed that population densities estimated from the largest forest fragments were reasonable approximations of densities in small forest fragments. We did not determine how lowering our estimates of N_c would affect extinction risk since uncorrected estimates of N_c were already so close to the quasi-extinction threshold in small forest fragments.

Because we observed very small populations of birds persisting in small fragments for long periods of time, we set the quasi-extinction threshold quite low, at two individuals. We suggest that a low threshold is appropriate given that six of our 14 study fragments were < 2 ha and population estimates based on observed densities were ≤ 6 individuals for each species on small forest fragments. Higher quasi-extinction thresholds (i.e., 20-100 individuals) can be set to account for demographic stochasticity and inbreeding, but a low quasi-extinction threshold is appropriate when population sizes are already very low (Morris and Doak 2002). For instance, PVAs of very rare species have set thresholds as low as one individual (Armbruster and Lande 1993, Burgess et al. 2007a).

We first validated the PVA for each species by determining the extent to which it correctly recreated historical patterns of extinctions observed on individual forest fragments. We

constructed a PVA for each species on each forest fragment ($n = 14$) and set the time horizon equal to the years since fragmentation, which was determined from historical records and interviews of village residents (Korfanta Chapter 2). For fragments > 29 ha, we used μ and σ_{ξ}^2 estimated for large forest fragments and for the remaining fragments, we used μ and σ_{ξ}^2 estimated for small forest fragments.

We then compared population projections from PVA with empirical patterns of species loss. We assumed that all species present on the largest forest fragments in the EUM and WUM were also present on small forest fragments immediately prior to habitat loss. Based on our banding data, we assumed that a species had gone extinct from a fragment if we captured ≤ 2 individuals in a given year. Although it is possible that more individuals occupied a fragment than the number captured, many of the study fragments were exceptionally small (particularly those where extinctions were observed) and we believe the banding data provide a reasonable characterization of local extinction. For individual species, we defined a PVA on a particular fragment as accurate when the species was absent and the estimated probability of extinction was > 0.50 , or where the species was present and the probability of extinction was < 0.50 . We defined a PVA as accurate and suitable for future extinction predictions for a species when it predicted at least 75% of historical population fates (extinction vs. persistence). To assess the overall reliability of the PVA to predict past extinctions across species, we compared current species number on each fragment with predicted species number using the function:

$$\sum_{i=1}^8 (1 - p_{ex})$$

where p_{ex} is the probability of extinction of species i .

For species with historically accurate PVA results, we estimated future extinction risk on small (2 ha), medium (34 ha), and large (704 ha) forest fragments, which represented the average patch size of our study site in each size class. We generated cumulative distribution functions (CDF) of extinction probability for each species for a 100 year time horizon. We were also interested in determining the minimum patch size that would be required to sustain each of the species with a 90% probability for the next 50 years. Thus, we also used PVAs to estimate extinction risk on a range of patch sizes, including 5, 10, 30, 50, 100, 200, 500 and 1000 ha. Similar to the historical validation PVAs, we used μ and σ_{Ξ}^2 estimates from small forest fragments for model fragments <30 ha, and we used μ and σ_{Ξ}^2 estimates from large fragments for fragments ≥ 30 ha. For historically validated species, we used a linear regression to assess the effect of body mass (g) and density (individuals/100 ha) on 100-year extinction risk for small, medium and large fragments.

RESULTS

Estimates of environmental variance associated with population growth rate varied widely, both among species and between small and large forest fragments (Fig. 2). A one-way ANOVA to test for differences in σ_{Ξ}^2 between fragment size classes showed significantly higher environmental variance on small fragments ($\overline{\sigma_{\Xi}^2} = 0.119$) than large ($\overline{\sigma_{\Xi}^2} = 0.030$) fragments ($F_{1, 14} = 5.08$, $p = 0.041$), even though the pattern was reversed in two species (Little Greenbul and Shelly's Greenbul). When converted to a percentage of the value of λ , $\overline{\sigma_{\Xi}^2}$ across species averaged 3.0% (range, 0.2 – 7.9%) on large fragments and 12.3% (range, 0.7 – 36.1%) on small fragments. Red-faced Crimsonwing showed the largest range in environmental variance, with 2.7% on large fragments and 36.1% on small fragments.

Historical validation of the PVAs showed a strong correspondence between the predicted and observed number of species on individual forest fragments (Fig. 3), although the PVA tended to overestimate extinction risk when all eight species were included. Because they did not successfully predict persistence or extinction on 75% of forest fragments, we excluded Little Greenbul, Olive Sunbird, and Shelly's Greenbul from further analyses. Most errors (97%) for all eight species represented cases where PVA predicted extinctions of populations that were still extant. We estimated future extinction risk for the five species for which PVA projection fit historical fragment-specific extinctions, including White-chested Alethe, Yellow-streaked Greenbul, Tambourine Dove, Striped-cheeked Greenbul, and Red-faced Crimsonwing.

Within 100 years, all five species had $\geq 98\%$ probability of extinction in small forest fragments (Fig. 5). On medium-sized fragments, the probability of extinction ranged from zero (Tambourine Dove) to 97% (Striped-cheeked Greenbul) and averaged 40% across species. On large fragments, extinction risk ranged from zero (Tambourine Dove) to 93% (Red-faced Crimsonwing) and averaged 30% across species. The minimum fragment size predicted to sustain all five species for 50 years with 90% probability was 290 ha (Fig. 6). Small sample size ($n = 5$) limited our power for detecting trends, but body size was not a significant predictor of extinction risk on small ($P = 0.592$), medium ($P = 0.241$), or large fragments ($P = 0.446$). Likewise, density was not a significant predictor of extinction risk on small ($P = 0.520$), medium ($P = 0.082$), or large fragments ($P = 0.078$).

DISCUSSION

Although the use of PVA has been challenged when data are limited (Ludwig 1999, Coulson et al. 2001, Sandercock and Beissinger 2002), our long-term study design provided a rare opportunity to generate and validate reliable extinction estimates based on empirical

estimates of population growth and environmental variance. The resulting PVAs are among the first to empirically predict a range of extinction probabilities within a single avian community and across a range of fragment sizes. Population viability analysis for understory birds in the East Usambara Mountains of Tanzania confirm a long faunal relaxation time (Tilman et al. 1994, O'Connell et al. 1998, Ferraz et al. 2003, Metzger et al. 2009) that will likely further reduce species richness in this important global biodiversity hotspot (Burgess et al. 2007b). Although high future extinction rates on very small (2 ha) forest fragments is not surprising, we found that population persistence is not assured for two relatively common species on medium (35 ha) and large (704 ha) forest fragments as well, and confirm that protection of even the largest remaining forest tracts may not be sufficient to maintain avian biodiversity in the long-term (Pimm and Raven 2000c). Elevated extinction risk was primarily attributable to depressed demographic rates, which did not necessarily track life-history correlates of extinction risk. Further, our results provided an empirical validation of extinction risk theory that suggests environmental stochasticity is elevated on small forest fragments and is an important driver of extinction risk for some species (Lande 1993, Saether et al. 2005). Together, these results suggest that when even limited demographic data are available, population viability analysis may be a powerful tool for estimating species-specific extinction risk and to better guide conservation strategies.

Feeding guild, density, and body mass did not predict extinction risk in individual species, although small sample size limited our ability to detect trends across species. The role of body size in extinction proneness is complex and often confounded with other variables (Henle et al. 2004, Sodhi et al. 2004), but some studies have found large-bodied species to be more extinction prone (Karr 1982, Castelletta et al. 2000). In this study, however, the largest of the five species (Tambourine Dove and White-chested Alethe) had the lowest extinction risk on

medium and large forest fragments, confirming earlier findings that extinction of Usambara bird species was not correlated with body mass (Newmark 1991). Also, certain feeding guilds such as terrestrial insectivores have been shown to be particularly sensitive to habitat fragmentation in the Usambara Mountains (Newmark 1991) and elsewhere (see Sodhi et al. 2004 for a review). In our current analysis, a granivore (Red-faced Crimsonwing) and a frugivore (Striped-cheeked Greenbul) had the greatest future extinction risks, while the terrestrial insectivore (White-chested Alethe) had lower risk. Thus, while ecological correlates may be helpful in describing broad extinctions patterns (Pimm et al. 1993, Sodhi et al. 2004, Lees and Peres 2008), they may be inaccurate when used to predict extinction risk in individual species.

A modified version of a relatively simple count-based PVA was accurate in recreating observed local extinctions for five of eight tropical understory bird species. For these species, patch size and attendant variation in demographic parameters (population density, population growth rate, and environmental variance) were sufficient to explain observed extinction patterns. PVAs overestimated extinction risk for species that disperse more readily among forest fragments, including Little Greenbul, Shelly's Greenbul, and Olive Sunbird. For these three species, we suggest that inter-patch movement of individuals likely prevents local extinctions through immigration (Brown and Kodric-Brown 1977) and that the individual forest fragment may not be the appropriate spatial scale for modeling population viability. Rather, a population is probably better defined as a collection of forest fragments well-connected by dispersal (Moilanen 2002) and a metapopulation PVA more accurately capture system-wide persistence (Akçakaya 2000). More importantly, overestimation of extinction risk for modestly dispersing species highlights the importance of dispersal in counteracting extinction risk associated with habitat fragmentation (Gascon et al. 1999, Sekercioglu et al. 2002, Van Houtan et al. 2007). This

result has an important conservation implication. Although many understory bird species are “psychologically flightless” (Diamond 1972) when confronted with gaps in forest habitat (Laurance 2004, Moore et al. 2008), improvement of dispersal via corridors may improve population persistence and should be considered in potential reserve designs.

Even within the same understory bird community, we found wide variation in extinction risk that was attributable to each species’ unique combination of population growth rate and its associated temporal variation (Fig. 5). The two species with the highest quasi-extinction risk across fragment size classes – Striped-cheeked Greenbul and Red-faced Crimsonwing – each had relatively low population growth rate and high 100-year quasi-extinction risk on medium and large fragments. However, Yellow-streaked Greenbul, with a similarly depressed population growth rate, had minimal short-term extinction risk on larger fragments due to lower environmental variance (in combination with higher population density). These results confirm the primacy of population growth rate in driving extinction risk (Saether et al. 2005), but also show the important role of environmental stochasticity in exacerbating that risk (Lande 1993, Melbourne and Hastings 2008).

Generally, tropical forest ecosystems have low environmental variability (Fjeldsa et al. 1997, Fjeldsa and Lovett 1997), but that stability may be offset by habitat fragmentation effects that tend to increase environmental stochasticity (Lande 1993). Although the intensity of environmental variance should be independent of population size (Lande 1993) small populations on habitat fragments may, nonetheless, experience elevated environmental stochasticity due to a range of abiotic and biotic edge effects, for instance (Woodroffe and Ginsberg 1998, Laurance 2002). When averaged across species, our results provide empirical evidence of elevated environmental stochasticity on small forest fragments relative to large

fragments (Fig.2). However, two species showed a reversal of that pattern and among the remaining species there was considerable variation in the magnitude of the fragmentation effect. Thus, in our study system, levels of environmental stochasticity appear to be quite species-specific. Without adequate population-specific data, researchers must occasionally make assumptions about the magnitude of environmental variance, for instance by assuming that temporal variance is a percentage of the population growth rate or another demographic rate (e.g., Haig et al. 1993, Gardner and Heinsohn 2007). Given the importance of environmental stochasticity in driving extinction risk and the range of variation in environmental variance that we estimated across species, our results confirm the importance of using empirically estimated and species-specific variance when possible (Saether et al. 2005).

Across a range of fragment sizes (10 – 1000 ha), the minimum patch size necessary for sustaining populations with 90% certainty for 50 years varied considerably across species, a finding also observed in other tropical systems (Watson et al. 2004). Based on the most extinction-prone species, Striped-cheeked Greenbul, we showed a minimum patch size requirement of 290 ha to sustain all five species with 90% probability. This is quite similar to the 302 ha minimum area required to maintain forest bird communities in isolated forest fragments in the KwaZulu-Natal midlands, South Africa (Wethered and Lawes 2003). A sharp decline in quasi-extinction risk between 10 and 30 ha for White-chested Alethe, Yellow-streaked Greenbul, and Tambourine Dove may have been an artifact of how we parameterized the PVAs, because we applied the same estimates of population growth rate and environmental variance to all fragment sizes > 29 ha. Although this was necessary because of the resolution of the data used to estimate population growth rate, these parameters were likely overestimated for smaller fragments within the “large” size class, while underestimating those parameters for the largest

fragments in that size class. Based on that assumption, quasi-extinction risk was probably underestimated for all species on mid-sized forest fragments. However, parameter estimates for all species were subject to this source of error and estimates of relative extinction risk across species should be valid.

Model assumptions

As with all models, PVA requires simplifying assumptions, violations of which can lead to over- or under-estimates of extinction risk (Morris and Doak 2002). First, we assumed that μ and σ^2 will not change with time due to density dependence, population size, or further habitat loss, for example. Although we did not have empirical data to model these effects, the small populations we observed on small forest fragments may be subject to Allee effects or demographic stochasticity. If so, these effects might increase extinction risk (Lande 1993, Holmes 2001). Second, we did not account for the possibility of catastrophes or bonanzas, which can either increase or decrease extinction risk (Ludwig 1999). However, the Eastern Arc Mountains have been shown to be ecoclimatically stable (Fjeldsa et al. 1997, Burgess et al. 2007b) and failing to model these rare events may be more accurate than including them with high error around model parameters. Although violations of these assumptions may color absolute estimates of extinction risk, we expect relative estimates to be robust to these assumptions (Sandercock and Beissinger 2002).

Conservation implications

At least two factors suggest that future extinction risk across the remaining understory bird community of the Usambara Mountains is greater than estimated for our five focal species. First, the five study species for which we modeled extinction risk were relatively abundant. In spite of their relative abundance, however, each of the five species had a high quasi-extinction

risk on small fragments and two of the species had a non-trivial extinction risk on even the largest forest fragments within the next 100 years. These results are cause for concern for less common species in the understory bird community, because rarity or small population size is often associated with extinction proneness (e.g., Pimm et al. 1988, Soule et al. 1988, Newmark 1991, Sodhi et al. 2004). Thus, our analysis likely underestimated overall risk in the understory bird community, particularly among dispersal-limited species. As a result, it seems likely that future species assemblages across all fragment sizes will be less diverse and populated by more common species.

The second factor that amplifies extinction risk is the potential for future landscape change. Although our analysis was predicated on the assumption that future landscape conditions will remain unchanged, human pressures on biodiversity hotspots, including the Eastern Arc, are predicted to increase (Cincotta et al. 2000). Indeed, human population density and infrastructure development are higher in the Eastern Arc than in sub-Saharan Africa (Burgess et al. 2007a), and like many other global biodiversity hotspots, annual growth rate of the human population is much greater than the world population growth rate (Cincotta et al. 2000). With more farmlands being created to support growing human populations (Burgess et al. 2007a), we can expect increasing pressures on remaining forests and avian biodiversity. Ultimately, the goal of biodiversity conservation in the Usambara Mountains must be weighed along with other societal needs. If conservation of the understory bird community is a priority, protecting remaining large forest tracts will be imperative but not sufficient. The capacity of forest fragments of all size classes to support dispersal-limited understory bird species would be improved with greater connectivity to other forest tracts. Ongoing initiatives to interlink the

largest blocks of forests in the EUM (Newmark 2002, Newmark et al. 2010), are a promising step in that direction.

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TABLES AND FIGURES

Table 1. Names, abbreviations, feeding guilds, estimated population density and weights for eight study species.

Family	Scientific name	Common name	Abbrev.	Feeding guild	Density (indiv/ 100 ha)	Avg. weight (g)
Columbidae (pigeons and doves)	<i>Turtur tymanistria</i>	Tambourine Dove	TD	Granivore	20	68.7
Pycnonotiidae (bulbuls)	<i>Andropadus virens</i>	Little Greenbul	LG	Frugivore	310	24.8
	<i>Andropadus masukuensis</i>	Shelley's Greenbul	SG	Frugivore	240	26.1
	<i>Andropadus milanjensis</i>	Striped-cheeked Greenbul	SCG	Frugivore	120	40.6
	<i>Phyllastrephus flavostriatus</i>	Yellow-streaked Greenbul	YSG	Insect gleaner/sallier	230	30.7
Turdidae (thrushes)	<i>Alethe fuelleborni</i>	White-chested Alethe	WCA	Terrestrial insectivore	180	54.0
	<i>Nectarinia olivacea</i>	Olive Sunbird	OS	Nectarivore	240	9.1
Estrildidae (waxbills)	<i>Cryptospiza reichenovii</i>	Red-faced Crimsonwing	RFCW	Granivore	80	12.3

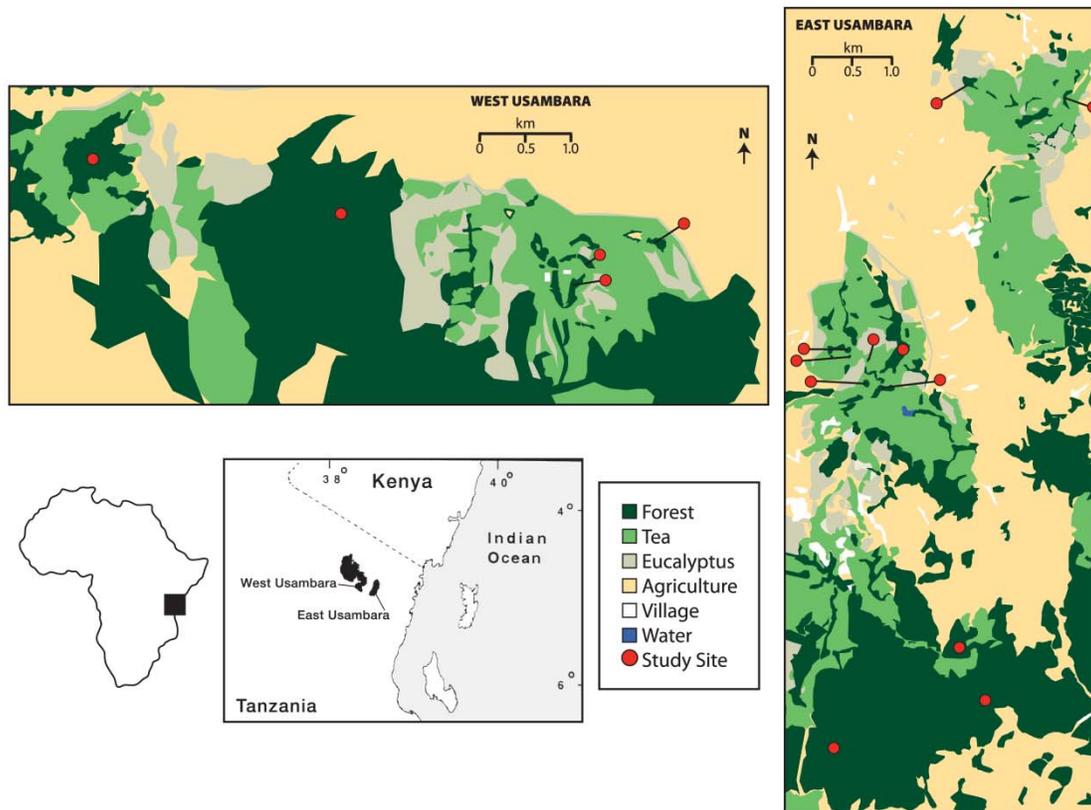


Figure 1. Land cover types and locations of study sites (1987-2008) in the East and West Usambara Mountains, Tanzania.

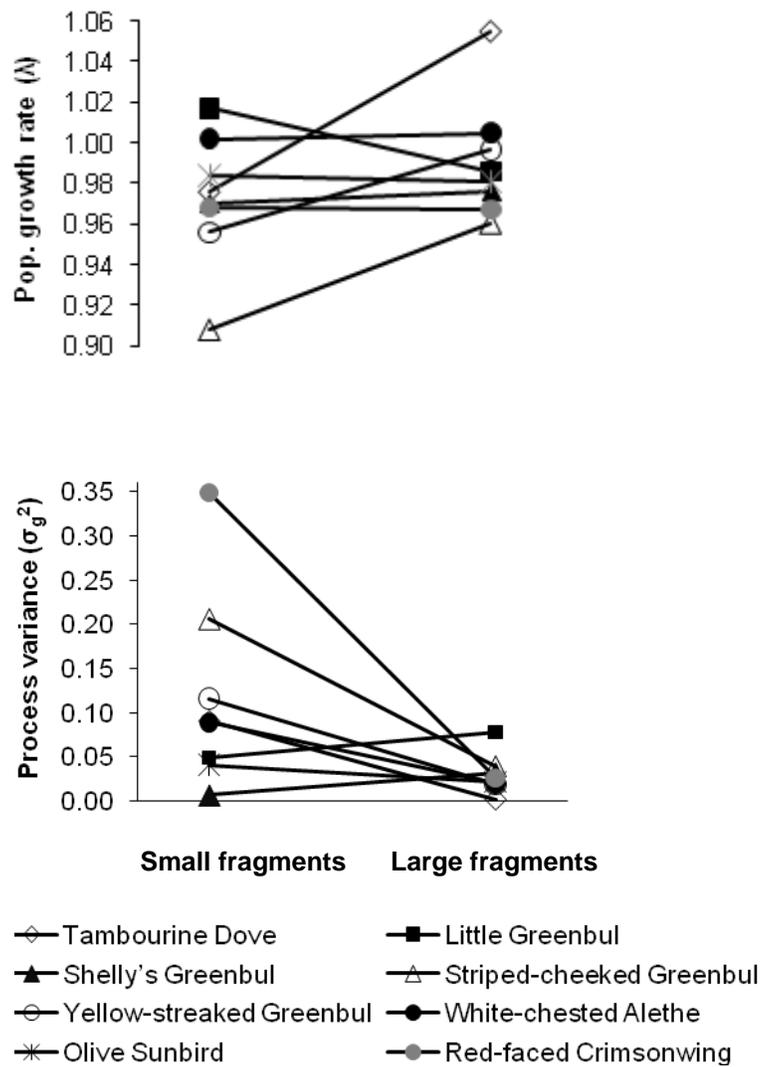


Figure 2. Observed population growth rate (λ) and associated environmental variance ($\sigma_{\mathbb{E}}^2$) estimates for eight understory bird species on small (0.2 – 5.5) and large (20 – 887 ha) forest fragments in the Usambara Mountains, Tanzania. Across species, $\sigma_{\mathbb{E}}^2$ was significantly higher on small forest fragments, while λ was not significantly different between the two size classes.

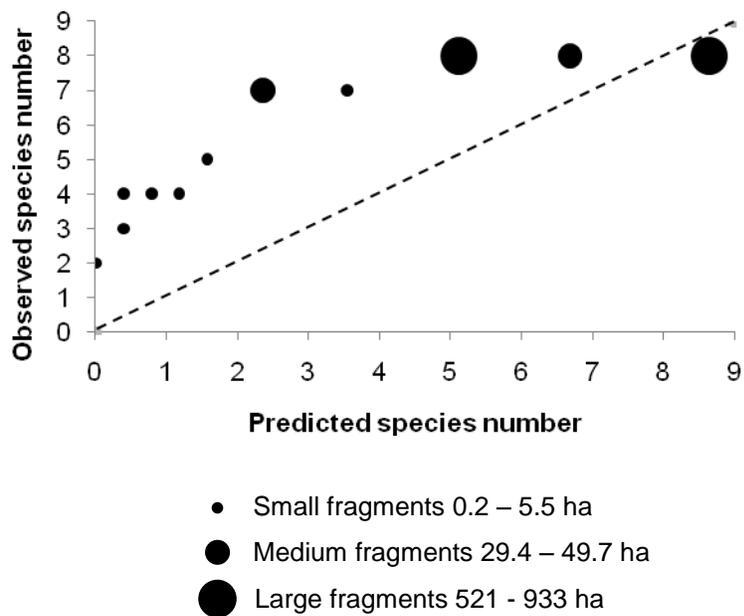


Figure 3. Historical validation of PVAs across eight understory bird species and 14 forest fragments of varying sizes in the East and West Usambara Mountains, Tanzania. Each point represents a forest fragment and shows the current number of species present versus the number of species predicted from PVAs. The line of equality shows perfect correspondence between observed and predicted species numbers. With all species included, the PVA showed strong correspondence between predicted and observed species numbers, although predicted extinction risk was generally higher than observed.

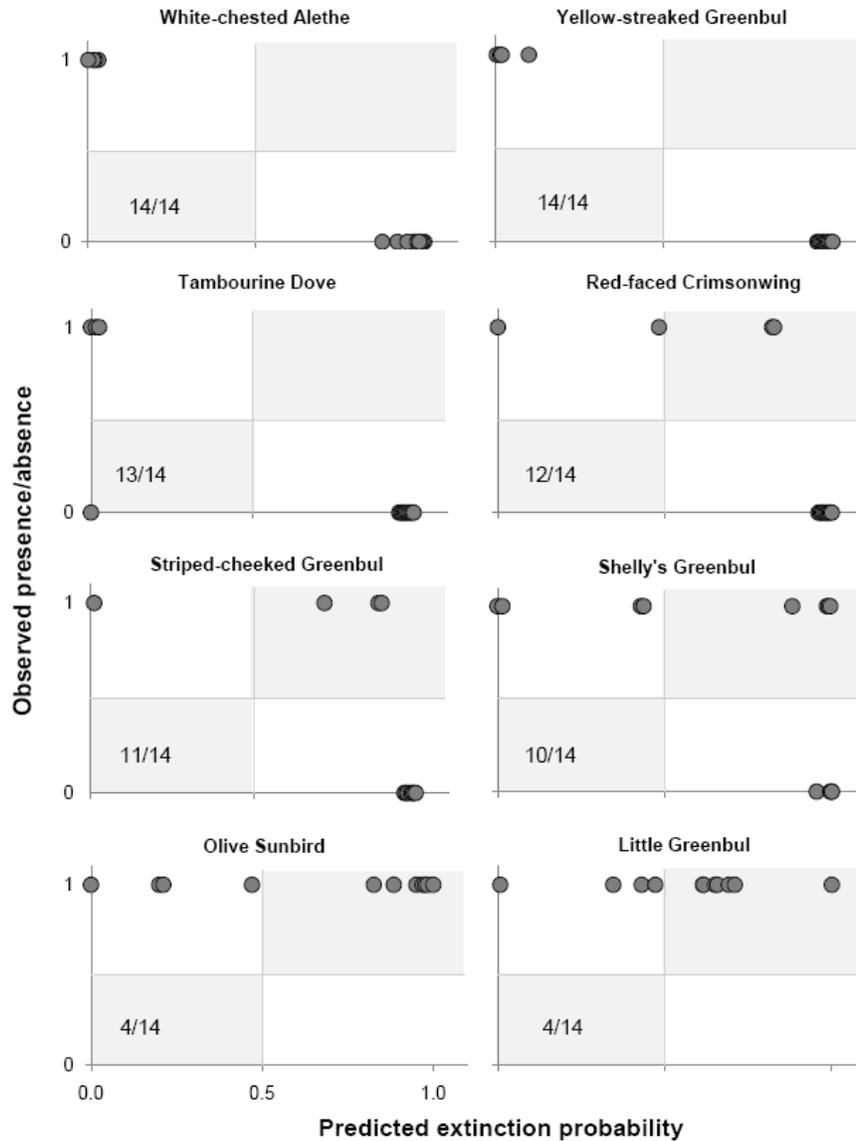


Figure 4. Historical validation of PVAs for each species on 14 forest fragments isolated for 40 to 115 years. Each point represents the PVA-predicted extinction risk versus the presence/absence of the species on each forest fragment. Ratios show the number of correctly predicted extinctions on the 14 fragments. Most incorrect points were for predicted extinctions in sites where species persist and were for more mobile species (Shelly's Greenbul, Olive Sunbird, and Little Greenbul).

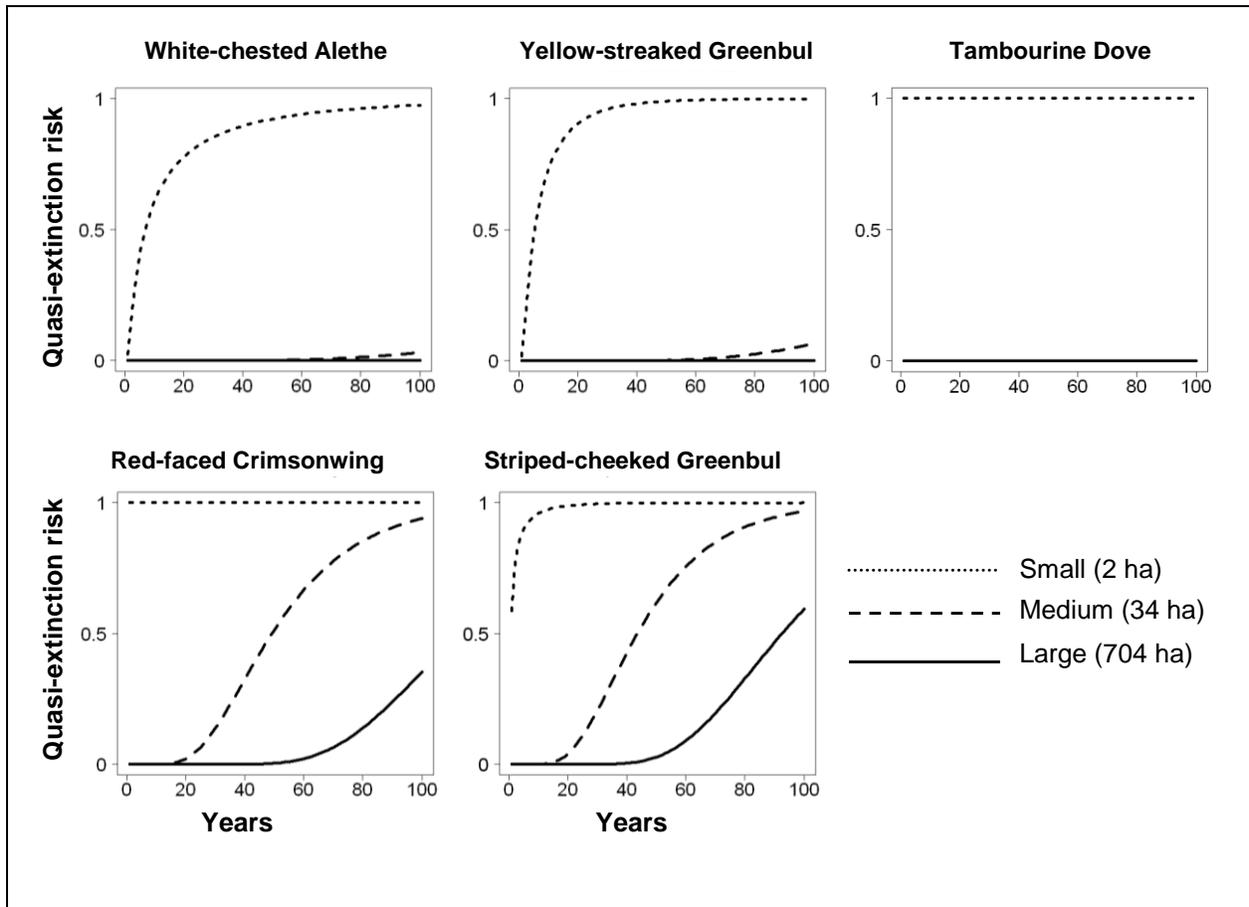


Figure 5. Cumulative distribution functions showing the probability of populations reaching ≤ 2 individuals on small, medium, and large forest fragments within 100 years. Quasi-extinction risk for Tambourine Dove on medium and large forest fragments was less than 10^{-10} . Because all species showed high quasi-extinction risk on small forest fragments, such fragment are unlikely to contribute to species persistence. Striped-cheeked Greenbul and Red-faced Crimsonwing also showed high quasi-extinction risk on medium-sized forest fragments.

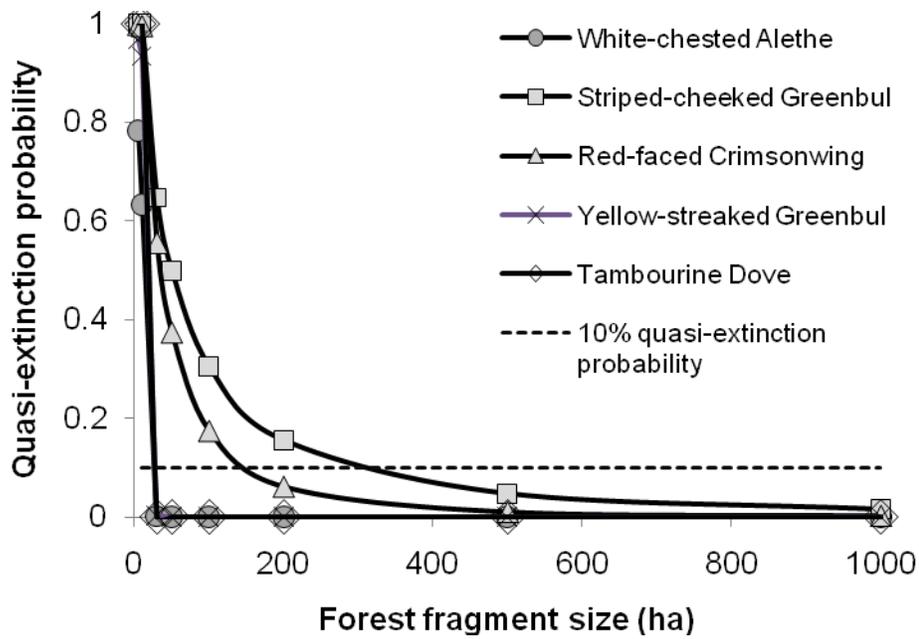


Figure 6. Predicted 50-year quasi-extinction risk for five understory bird species across a range of fragment sizes. All species have $\geq 90\%$ probability of persistence on forest fragments ≥ 290 ha.

CHAPTER FOUR

Multi-site PVA at the community level: using demography to guide reserve design in a biodiversity hotspot

ABSTRACT

Ongoing tropical forest fragmentation threatens to exacerbate local and range-wide extinctions of understory bird species in Afrotropical landscapes and elsewhere. Reserve networks that protect forest habitat, as well as promote dispersal between forest remnants via corridors, are among the most promising opportunities for long-term conservation. With long-term demographic data rarely available for multiple species of conservation concern, reserve designs are frequently guided by species richness metrics or single-species viability analysis. Consequently, persistence, which is one of the most important conservation metrics, is rarely evaluated for the full suite of species reserve networks are designed to conserve. We used count-based, multi-site population viability analysis to assess extinction risk for 14 understory bird species under four realistic reserve scenarios intended to slow biodiversity loss in the highly-fragmented East Usambara Mountains, Tanzania, a global biodiversity hotspot. Across species, the most protective of the reserve designs would delay quasi-extinction risk by an average of 28 years, providing a longer time horizon to implement additional conservation strategies. A number of conservation implications were revealed by our multi-species demographic analysis that might not be evident from traditional approaches. The effect of increased dispersal in reserve designs that enhanced connectivity was generally but not always positive, suggesting that the configuration and size of fragments to be connected may affect extinction risk. Extinction risk was highly variable among species, a finding that cautions against single-species approaches that tend to over- or under-estimate the value of the reserve to species not directly evaluated.

Finally, comparison of demographic results with species-area curves generated for the same avian community showed that species-area curves substantially overestimated post-fragmentation species richness relative to a demographic approach. Our finding of high extinction risk for many species across a range of real-world conservation alternatives suggests that a large extinction debt is still yet to be paid in this, and possibly other, biodiversity hotspots that have experienced extensive habitat loss. Future extinctions will not be entirely curtailed through protection of remaining habitat alone, and might only be reversed through improvements to habitat quality in addition to the creation of new reserves.

KEYWORDS

Population viability analysis, demography, environmental stochasticity, understory bird, metapopulation, reserve design, biodiversity hotspot, Eastern Arc, Usambara Mountains

INTRODUCTION

Habitat destruction is the primary driver of the biodiversity crisis (Pimm and Raven 2000b), which is defined by contemporary global extinction rates that are two to three orders of magnitude greater than historic extinction rates (Pimm et al. 1995, Dirzo and Raven 2003). Even more pervasive are local and regional extinctions that may alter community dynamics and ecosystem function, and population declines that are characteristic of the majority of higher taxa species (Stork 2010). Nowhere is the biodiversity crisis more evident than in the tropical forests that support half or more of global biodiversity (Raven 1980, Wilson 1988) but which are being lost at an estimated 1.2% per year (Whitmore 1997). Indeed, of the 25 biodiversity hotspots identified as conservation priorities based on levels of endemism and habitat loss, 17 are in tropical forests where less than 12% of primary forest remains (Pimm and Raven 2000b, Bishop and Myers 2005). To slow biodiversity loss in such areas, non-governmental organizations and

others have proposed enhanced protection of high-priority conservation locations (O'Connell et al. 1998). While large reserve networks represent great promise for long-term conservation (Peres 2005), and significant funding is directed to those efforts (O'Connell et al. 1998, Bishop and Myers 2005), the ability of such conservation efforts to reduce extinctions and slow biodiversity loss remains to be evaluated.

Population viability analysis (PVA) is among the most useful tools for predicting relative extinction risk of individual species under a range of reserve scenarios (Lindenmayer et al. 2002, Morris and Doak 2002) and has been used in several well-studied species (Armbruster and Lande 1993, Lindenmayer and McCarthy 2006, Burgess et al. 2007b). However, the long-term demographic data required to construct reliable PVAs are not available for most species, and as a result, assessments of species persistence are rarely incorporated into reserve planning (O'Connell et al. 1998, Cabeza and Moilanen 2001). The challenge of data limitations is particularly acute in understudied tropical ecosystems (Sodhi 2008). In many such regions the effectiveness of reserves is typically measured in snapshot characterizations of species representation, usually in the form of species richness (Rodrigues et al. 1999, Araújo and Williams 2000, Gaston et al. 2002). While establishing reserves around the current or potential distribution of species is a reasonable approach in the absence of demographic data, it can be risky without knowledge of whether populations in those locations are stable or declining (Van Horne 1983, Pulliam 1988, Abrams 2002, Salomon et al. 2006). In fact, previous work has shown that efficient reserve designs that maximize diversity while minimizing reserve area (Gaston et al. 2002), may show considerable species loss over time since persistence does not necessarily follow from simple representation (Margueles et al. 1994, Virolainen 1999, Rodrigues et al. 2000). When data are available, incorporating population viability analysis into

reserve design can improve likelihood of conserving species in the long-term (Cabeza and Moilanen 2001).

The effect of reserve design on species persistence depends on the spatial configuration of populations and the biology of the species of conservation concern. By definition, biodiversity hotspots have experienced exceptional habitat loss (Bishop and Myers 2005). Particularly in tropical forests, habitat loss is also accompanied by fragmentation that may isolate populations to an extent that depends on the composition of the matrix and the willingness of individuals to cross non-forested habitat (Laurance et al. 2002, Van Houtan et al. 2007). For many species that have evolved under conditions of continuous forested habitat, such as forest understory birds, gaps in the forest may constitute real barriers to dispersal and populations may become effectively isolated on disjunct forest fragments (Moore et al. 2008). Thus, extinction risk may be elevated in small and isolated populations that experience greater environmental and demographic stochasticity (Lande et al. 2003). Extinction risk also increases with correlation of growth rates of disconnected populations due to shared environmental conditions which are generally more similar among geographically proximate populations (Harrison and Quinn 1989, Hanski and Woiwood 1993, Hilderbrand 2003, Vuilleumier 2007). Such population synchrony and attendant extinction risk may also increase with dispersal, which is often facilitated in reserve design via corridors designed to connect otherwise-isolated forest fragments (Hilty et al. 2006). Importantly, however, corridors also confer an important benefit by promoting rescue effects (Brown and Kodric-Brown 1977, Stacey and Taper 1992). Together, the effects of dispersal and spatial correlation combine in unique ways, making their effects on extinction risk difficult to predict without biologically realistic population projections (Tilman et al. 1994,

Higgins 2009). Thus, efficacy of reserve designs would benefit from population viability analyses that can account for variation in spatial configuration of conserved fragments.

Integrating extinction risk into reserve planning is most needed in the tropical forests where biodiversity is the richest, extinction rates are the highest, and remaining forests are most at risk (O'Connell et al. 1998, Gascon et al. 1999, Burgess et al. 2007b). Similar to tropical forests world-wide, the East Usambara Mountains (EUM) of northeast Tanzania have undergone extensive deforestation, leaving isolated forest fragments in a matrix of agricultural land uses (Hall et al. 2009). Consequently, many species have gone locally extinct from small forest fragments (< 30 ha) and some species appear to be extinct regionally across the EUM (Newmark 1991). Previous analyses have also shown persistent demographic consequences of fragmentation, with significantly lower apparent survival and population growth rate on small forest fragments among > 20 avian species, even 40-115 years after initial deforestation (Korfanta chapter two). Together with evidence of more recent extinctions (described below), these results suggest ongoing faunal relaxation in the EUM and a high likelihood of further species losses. A similar extinction debt is characteristic of avian communities in tropical forests world-wide (Tilman et al. 1994, O'Connell et al. 1998, Ferraz et al. 2003) and is compounded by ongoing habitat loss in many areas (Burgess et al. 2007b). Thus, while we strive to protect remaining biodiversity with ambitious global biodiversity reserves, many populations may be on a trajectory toward extinction in spite of these best efforts. In the EUM, as in other critical biodiversity locations, demographic analyses can identify the most imperiled members of community and help refine reserve designs to reverse or slow species loss.

To protect and restore populations in this biodiversity hotspot (Bishop and Myers 2005), the Tanzanian government and its partners are considering several ambitious reserve scenarios,

which would connect up to 11 of the remaining large forest blocks in the EUM with wide (1 km) forested corridors. Because many of the understory bird species in this system cross forest gaps at extremely low frequency, if at all, forested corridors are required to restore functional connectivity in the landscape (Newmark 1992). But such initiatives bear considerable financial costs associated with land acquisition, forest restoration, and reserve management. Reserve establishment and management is particularly expensive in biodiversity hotspots like the Eastern Arc (Balmford et al. 2001). Additionally, some corridor options under consideration require displacement of residents or loss of agricultural land uses (United Republic of Tanzania 2006), creating a range of social costs as well. Consequently, the potential benefits of the reserve scenarios to biodiversity conservation should be well-calculated and based on the best available biological evidence.

In this study, we combine long-term demographic data to model the persistence of understory bird species across a range of conservation scenarios proposed for the EUM. To our knowledge, this is the first application of a multi-species PVA to reserve design in a global biodiversity hotspot. Although negative population growth rates, even on large forest fragments, predict population declines for most species (Korfanta chapter two), ultimate extinction is not a *fait accompli*. Rather, an enhanced reserve network may delay or minimize extinction risk. However, as with many other biodiversity hotspots, the relative conservation benefits of the EUM reserve designs under consideration have not been quantified. Our objectives were to 1) characterize the range of extinction probabilities across 14 species representing a range of life-history attributes and demographic rates, 2) determine the relative effectiveness of four reserve design scenarios in conserving the understory bird community of the EUM, and 3) determine

how demographic data alter or confirm projected biodiversity loss from traditional species-area approaches.

METHODS

Study area and reserve options

The EUM consists of lowland (200-800 m) and sub-montane (800-1,200 m) forest that has undergone an estimated 73% loss during the last century primarily due to land clearing for small- and large-scale agriculture (Moreau 1935, Newmark 2002). Remaining forest now exists as mostly isolated remnants with abrupt forest boundaries adjacent to agriculture. Most of the largest ($\approx 200 - 8,000$ ha) fragments are managed by the Tanzania Forestry Division as nature or forest reserves where timber extraction is forbidden and where land is primarily managed for biodiversity conservation and water catchment purposes (Balmford et al. 2001, Burgess et al. 2007b) (Fig. 1).

We examined four realistic reserve design scenarios that reflect a broad range of options available to the Tanzanian government and other important stakeholders (Fig. 2). Scenario 1 – the current state -- represents the current state of protection for the eleven major forest blocks. Although several of the forest blocks/reserves are bordered by by non-protected forested land which can serve as important movement corridors among reserves, this latter forest was excluded under this scenario because of the presence of large gaps and the high risk that these forests face from development. Scenario 2 – the submontane corridor option -- represents the current state of reserves plus a protected forested corridor connecting the Amani and Nilo Nature Reserves. The submontane corridor would encompass the recently gazetted Derema Forest Reserve/Corridor and existing non-protected forest lands that extend between Derema FR and the Nilo Nature Reserve /Corridor. Scenario 3 – the submontane plus four corridors option --

includes the submontane corridor included in scenario 2 and four additional corridors that local NGO's are attempting to protect and would connect nine forest and nature reserves. Finally, Scenario 4 – the fully connected scenario – would connect all major forest blocks via 11 separate corridors. The forest reserves and proposed corridors range in elevation from $\approx 160 - 1,500$ m.

Based on previously developed recommendations, we assumed each corridor would be 1 km wide, based on habitat requirement of a highly area-sensitive understory bird species, the Usambara Thrush (*Turdus abyssinica*) (Newmark 1993). A 1 km-wide corridor would provide a 200 m buffer around a 600 m core, which in turn was estimated by doubling the median distance of encounter of individuals captured furthest from the forest edge. Because of the substantial width of proposed corridors, we assumed that area and forest availability in corridors would provide suitable nesting and foraging habitat, and would facilitate dispersal between adjacent reserves (Newmark et al. 2010). Corridors currently used for agriculture or other non-forested land cover types may be passively revegetated or actively restored to forest, with either option requiring some amount of time before habitat is usable by understory birds. Although we recognize the necessary time delay required for new corridors to become effective, we assumed that corridors will be actively revegetated to forest plant species and that they will be available to understory birds immediately.

Study species

We estimated extinction risk for the 14 understory bird species for which we had sufficient, long-term demographic data to parameterize a PVA (Table 1). Because previous analyses showed that count-based PVAs were most accurate for sedentary species (Korfanta chapter two), we focused our analyses on dispersal-limited species. These species were never, or rarely, recaptured outside of their original capture site and have not been observed foraging or

moving through non-forested matrix (Nichols et al. 1998, Borghesio et al. 2008). The 14 species spanned five feeding guilds and ranged in population density (Table 1) and demographic response to forest fragmentation (Korfanta chapter two). The species also varied in their elevational ranges (Stuart 1991), which we classified as low-high ($\approx 150 - 2,250$ m), mid-high ($\approx 450 - 2,250$ m) and high (> 900 m). Because of elevational distributions of species, we assumed that not all reserves and corridors would be available to species in each elevational class (Fig. 2). Thus, for species restricted to high elevations, for instance, Scenarios 2-4 were effectively the same because connected forest reserves were generally < 900 m in elevation.

PVA model structure

Count-based PVA is a powerful and convenient tool to stochastically model persistence of local populations from estimates of population growth rate and environmental variance – parameters that may be estimated from readily available annual count data (Dennis et al. 1991, Morris and Doak 2002). However, when a reserve comprises multiple sites, as do the EUM reserve scenarios, simple count-based methods may not capture the important effects of correlated growth rates or dispersal of individuals among populations (Dennis et al. 1998, Akçakaya 2000). Count-based PVAs typically model individual sites separately, assuming complete independence of populations, or lump all sites together in a single hypothetical reserve that assumes complete correlation and population mixing (Hinrichson 2009). However, if growth rates of disconnected populations are correlated, extinction risk will be underestimated under the assumption of independent populations (Harrison and Quinn 1989, Hanski and Woiwood 1993, Hilderbrand 2003, Vuilleumier 2007). The effect of dispersal on extinction risk is more complex and results in an extinction risk trade-off between increased population synchrony and a potential rescue effect (Brown and Kodric-Brown 1977, Tilman et al. 1994,

Hanski 1998, Burgess et al. 2007a). As an alternative, multi-site, count-based PVA may be used to estimate extinction risk from count data while also considering dispersal and correlation among populations (e.g., Dennis et al. 1998).

We constructed a multi-site, count-based PVA to estimate reserve-wide extinction risk for each species across the four reserve scenarios. We treated each population within a nature reserve, forest reserve, or corridor as a separate subpopulation, i , with a starting population size, $N_{i,0}$. To incorporate environmental stochasticity in each year of the model, we estimated $N_{i,t+1}$ as the product of $N_{i,t}$ and a randomly determined estimate of annual population growth rate for that subpopulation, $\lambda_{i,t}$. The set of $\lambda_{i,t}$ values for all subpopulations in a given year were determined by first drawing a set of $\log(\lambda_{i,t})$ values from a single multivariate normal distribution. We thus assumed that λ_i values were log-normally distributed and had the potential to be correlated across time. While this process is density-independent, we also set a maximum population density cap, K_i , in each subpopulation, to prevent unrealistic densities from occurring. As described below, we also included parameter estimation uncertainty in both the mean and variance of $\log(\lambda_{i,t})$ values into our simulations (Doak et al. 2005).

We modeled the effect of dispersal by multiplying the vector of $N_{i,t+1}$ values by a dispersal matrix to account for both immigrants to, and emigrants from, each population. The dispersal matrix included a single dispersal estimate for each possible population pair (i.e., those that were adjacent). An inconvenient problem results from having constant probabilities of dispersal between different-sized patches with uncorrelated growth rates. In this case, a ‘penalty’ arises when a small patch can receive so many dispersers that they exceed the local patch density cap (K_i). To prevent this, we adjusted the dispersal rates between patches such that

no patch could receive more dispersers than the maximum number needed to reach the dispersal cap following population growth for a year, but prior to dispersal out of the patch.

Following dispersal, we applied the density cap (K_i) for each population by setting $N_{i,t+1} = K_i$, when $N_{i,t+1} > K_i$. For each species, we set a quasi-extinction threshold of 20 for the entire reserve network. Because dispersal from connected populations could theoretically repopulate extinct populations, we grouped connected populations into blocks. Blocks could only go extinct when the combined population sizes of all reserves within the blocks was < 2 , and once a species was extinct from a block, it could not be repopulated, reflecting the improbability of inter-patch dispersal in the absence of a corridor. We estimated cumulative extinction risk for each combination of species, scenario, and environmental variance, based on 2,000 simulations of the model for 200- and 1000-year time spans. Although we recognize that the predictive accuracy of the model declines with longer time spans, we used 1000-year runs to estimate the year of 50% quasi-extinction risk. This metric allowed us to compare scenarios for those species that showed zero extinction risk in the 200-year time span. We also estimated average 100-year quasi-extinction risk across species to compare predictions from demographic analyses to projections from previously generated species-area curves for the same time span (Pimm and Raven 2000b).

Parameter estimation

For each reserve or corridor, we estimated $N_{0,i}$ as the product of species density and reserve area (Table 1). To estimate density for each species, we used spot mapping at multiple study sites in the EUM during the 2008 breeding season. We mapped the estimated locations of singing and sighted birds as a perpendicular distance to the nearest trail marker located at 25 m intervals within a 50 m grid, and estimated average individuals/100 ha based on the resulting

territory map. Based on our capture rates in small forest fragments where populations are often more dense, we estimated K as twice the value of $N_{0,i}$.

We used mark-recapture analysis to estimate population growth rates (λ) for each species. Annually, from 1987-2008, WDN has used mist nets to monitor populations of understory birds in 14 forest fragments in the East (EUM) and West Usambara Mountains (WUM), which are adjacent but disconnected mountain ranges. Study fragments ranged in size from 0.2 - 886.8 ha (see Korfanta chapter two for more detail) and had been isolated for 40-115 years. Because of similar bird communities within fragments 29.0 – 886.8 ha, we categorized the four fragments > 29.0 ha as large and the remaining 10 fragments as small. One of the study fragments, the Amani Nature Reserve (NR), was within the proposed reserve system and all other fragments were adjacent but not included in the reserve system. Full sampling methodology is available in Korfanta (chapter two).

Count-based PVAs are typically constructed from abundance time series data used to estimate the mean and variance, μ and σ^2 , of the instantaneous population growth rate ($\log(\lambda)$) (Dennis et al. 1991); however, in our case, data were not sufficient to estimate either of these parameters from estimates of annual population size. Instead, we used data from the entire study period ($n = 22$ years) to generate a single estimate of mean λ , $\bar{\lambda}$, for each species in the Amani NR. We assumed that λ estimates drawn from Amani NR were representative of the remaining unsampled reserves, which were also large (> 29 ha, excluding the ≈ 4 ha Manga-Bamba Ridge corridor) and in the same mountain range as the study site. To estimate $\bar{\lambda}$, we used Pradel's subroutine in Program MARK, a reverse-time approach that estimates λ based on estimates apparent survival (Φ) and recapture rate (p). We used the best fit model of Φ based on data from all study sites and including fragment size and landscape (EUM vs WUM) effects. We modeled

p as constant among sampling years (complete analysis methodology is described in Korfanta chapter two). Although data from all study sites and two landscapes (EUM and WUM) were used to estimate Φ as accurately as possible, we estimated λ specifically for Amani NR. We then used the estimate of $\bar{\lambda}$ to estimate μ and σ^2 , assuming that $\log(\lambda)$ values are normally distributed:

$$\mu \cong \ln \bar{\lambda} - \frac{1}{2} \ln \left[\left(\frac{\text{var} \bar{\lambda}}{\bar{\lambda}^2} \right) + 1 \right]$$

$$\sigma^2 = \ln \left[\left(\frac{\text{var} \bar{\lambda}}{\bar{\lambda}^2} \right) + 1 \right].$$

These expressions rely not just on an estimate of $\bar{\lambda}$ but also on the sampling variance of $\bar{\lambda}$, $\text{var} \bar{\lambda}$, estimated as:

$$\text{var} \bar{\lambda} = \frac{(\lambda \sigma_{\text{total obs.}}^2 - \lambda \sigma_{\text{process}}^2)}{n}$$

where n was the number of years used to estimate $\bar{\lambda}$. We used the ‘variance components’ procedure in Program MARK (Dinsmore et al. 2002) to estimate total observed variance ($\lambda \sigma_{\text{total obs.}}^2$) and process variance ($\sigma_{\text{process}}^2$) of σ^2 based on time-dependent models that estimated λ annually. Because we were unable to produce reasonable estimates of λ for missing sample years when using the entire 22-year dataset, we estimated $\text{var} \bar{\lambda}$ from a nine-year period of (1992-2000) for which we had annual sampling records across all sites. Data were sufficient to estimate $\text{var} \bar{\lambda}$ directly for four species: White-chested Alethe (*Alethe fuelleborni*), Yellow-streaked Greenbul (*Phyllastrephus flavostriatus*), Tambourine Dove (*Turtur tymanistria*), and Striped-cheeked Greenbul

(*Andropadus milanjensis*). Data were not sufficient to estimate $var\bar{\lambda}$ directly for the remaining nine species. For those species, we applied the low (0.002), mean (0.030), and high (0.078) estimates of $var\bar{\lambda}$ previously estimated for a suite of different understory bird species in the same avian community (Korfanta chapter three). That suite included the four species listed above and four additional species not included in this reserve analysis (*Cryptospiza reichenovii*, *Nectarinia olivacea*, *Andropadus virens*, and *A. masukuensis*). We believe these estimates of $var\bar{\lambda}$ are reasonable approximations of true process variance for the study species because the surrogate species were members of the same understory bird community and shared the same physical environment over the same time frame.

To include parameter estimation uncertainty for σ^2 in our simulations, we estimated the sampling variance around σ^2 as:

$$\sigma_{var}^2 = \frac{2 * n * \sigma^{2^2}}{(n - 1)^2}$$

where n was the number of samples ($n = 9$ years) used to estimate σ^2 . We used this variance with an assumed Chi-square sampling distribution for variance to simulate random σ^2 values (Dennis et al. 1991, Morris and Doak 2002). Because we were only able to estimate process variance and associated sampling variance for four species, we used the highest estimate of σ_{var}^2 (0.000380) for the ten remaining species.

As noted above, in each year of a simulated population trajectory, we drew random variates from a multivariate normal distribution to generate $\log(\lambda_{i,t})$ values, which we then exponentiated to generate the corresponding $\lambda_{i,t}$ estimates. To incorporate parameter uncertainty into this process, for each replicate simulation, we began by choosing a pair of μ and σ^2 values

from the sampling distribution of each. These were then used for the duration of that temporal simulation.

We used a multistate model within Program MARK to estimate the probability of individuals dispersing across varying distances between sites within contiguous forest during the period, 1989-2008. Because dispersal rates are extremely low in these species and we were unable to estimate species-specific dispersal, we combined all 14 species into a single multistate model: $\Phi(\text{survival category}) p(.) \Psi(\text{possible site pairs})$, where Ψ was the probability of moving between sites. Species were assigned to categories of moderate (0.626 – 0.651) or high (0.713 – 0.786) apparent survival based on previous estimates (Korfanta chapter two). We modeled recapture rate (p) as constant and we estimated dispersal probability (Ψ) for three distances (325 m, 750 m, and 1100 m), which represented the distances between study sites separated in the Amani Nature Reserve.

We then used Ψ estimates from the multistate model to calculate approximate dispersal probabilities for the PVA model. We assumed that the probability of an individual dispersing to a neighboring reserve or corridor decreased with increasing distance from the boundary. To calculate a single dispersal probability for all individuals within a reserve, we estimated the proportion of the total reserve within varying distances of the reserve boundary -- 0 - 400 m, 401 – 800 m, and > 800 m – and assigned our corresponding dispersal estimates (at 325 m, 750 m, and 1100 m) to each zone. We then estimated the dispersal probability of the reserve as the product of the proportion of the total reserve in each zone by the dispersal estimate for that zone. Thus, the per-capita probability of an individual dispersing from a large reserve was less than the dispersal rate from a smaller reserve. We used these estimates to construct a dispersal matrix

with an estimate of dispersal for all population pairs, although we precluded gap-crossing dispersal by only allowing dispersal to occur between adjacent, connected reserves and corridors.

In addition to dispersal, multi-site PVA can also account for spatial correlation of populations. Because data were not sufficient to test for spatial correlation based on estimates of λ for each population and year, we instead used raw counts of captures on the two largest fragments separated by $\approx 3\text{km}$ for the 11 years during which both fragments were sampled. We used a Pearson correlation statistic to test for correlation of capture numbers by year.

The benefits of our PVA model could be derived from both an increase in area and enhanced dispersal, both of which would result from the creation of wide, forested corridors. To tease apart these effects, we ran models with and without dispersal, while allowing habitat area to increase as proposed under each scenario. We used a paired-t test within each species to determine differences in 200-year extinction risk for models with and without dispersal.

To determine the relative importance of a range of model parameters in affecting extinction risk, we used a linear model to determine the amount of total variance (sum of squares) explained by μ , σ^2 , scenario, population density, average mass, elevational range, and the interactions of these terms on $\ln(\text{extinction risk})$. For this analysis, we defined extinction risk as the average year at which a population reaches 50% extinction risk.

Comparison of species loss from demographic and species-area approaches

We compared estimates of biodiversity loss projected from the classic species-area relationship to a demographic approach based on species-specific extinction risk averaged across species. To account for a time lag between initial habitat loss and relaxation to a new post-fragmentation species number, we used a variation of the species-area curve by Brooks et al. (1998) to estimate final post-fragmentation species richness in the EUM (S_{frag}):

$$S_{frag} = \left(\frac{A_{frag}}{A_{tot}} \right)^z * S_{tot}$$

where A_{frag} was the remaining forest habitat in the entire EUM, A_{tot} was the original forest habitat prior to habitat loss, z was the exponential decay constant, and S_{tot} was the pre-fragmentation community size. We estimated A_{frag} as 32,749 ha based on the sum of areas for existing forest and nature reserves (Johansson and Sandy 1996) and we estimated A_{tot} as 58,480 ha based on previous estimates of percent deforestation in the EUM (Newmark 2002). We assumed a starting community size (S_{tot}) of 51 forest-dependent understory birds based on our mist netting records, spot mapping, and the findings of Borghesio et al. (2008). In light of our uncertainty about the appropriate z value for our system, which varies as a function of fragment size and continuity (Lomolino et al. 1989, O'Connell et al. 1998), we projected species richness based on two z -values – 0.15 and 0.25.

To project ultimate species richness from demographic data, we estimated the average extinction risk across the 14 study species under the most optimistic conditions by assuming full habitat connectivity (Scenario 4) and low environmental variance. We assumed that average extinction risk of the 14 study species was a reasonable approximation of the larger understory bird community since the study species spanned life history attributes; however, we recognize that extinction risk may in fact be higher in rarer species not represented in the demographic analysis. Thus, our demographic approach likely yielded a conservative estimate of future species loss. From demographic data, we estimated future species richness as:

$$S_{frag} = S_{tot} - (S_{tot} * \bar{E}_{200})$$

where \bar{E}_{200} was average 200-year quasi-extinction risk across species.

RESULTS

Dispersal probability declined rapidly with distance between sites; probabilities were 0.145, 0.012, and 0.002 for sites separated by 325, 750, and 1100 m, respectively. Capture numbers between sites were not significantly correlated for any of the species ($P < 0.05$), nor were captures correlated when all species were combined into a single analysis (Pearson correlation = -0.117, $P = 0.731$). As a result, we did not include spatial correlation in the PVA.

Across species, 100-year quasi-extinction risk averaged 19.7%, 22.3%, and 31.3% under conditions of low, mean, and environmental variance. Half of the species ($n = 7$) had $> 75\%$ probability of quasi-extinction within 200 years given the current amount and configuration of habitat (Scenario 1) in the East Usambara Mountains. These high-risk species included Tiny Greenbul, Striped-cheeked Greenbul, Orange Ground Thrush (*Turdus gurneyi*; under conditions of high σ^2), Usambara Thrush (*Turdus abyssinica*), Yellow-throated Woodland Warbler (*Phylloscopus ruficapilla*, when σ^2 was high), Spot-throat (*Modulatrix stictigula*), and Red-capped Forest Warbler (*Orthotomus metopias*). Greater connectivity and area of the three alternative reserve scenarios resulted in a reduction of the number of high-risk species to five (the previous list minus Yellow-throated Woodland Warbler and Orange Ground Thrush). Across species, the four scenarios varied in their average estimates of mean time to 50% probability of quasi-extinction, with Scenario 1 resulting in the shortest time horizon and the most connected scenario having the longest time horizon (Fig. 3). The highest degree of protection (Scenario 4) conferred a benefit of 27.5 additional years in average time to reach 50% quasi-extinction risk relative to Scenario 1 (paired-t test: $t_{29} = -3.31$; $P = 0.002$) (Fig. 3). Scenario 1 also showed significantly shorter mean time to 50% quasi-extinction risk relative to Scenario 2 (paired-t test: $t_{29} = -3.81$, mean difference = 10.27; $P = 0.001$) and Scenario 3 (paired-t

test: $t_{29} = -3.83$, mean difference = 10.53; $P = 0.001$). Scenario 2 was not significantly different from Scenario 3 (paired-t test: $t_{29} = -0.19$, mean difference = 0.27; $P = 0.849$), but had shorter time to quasi-extinction than Scenario 4 (paired-t test: $t_{29} = -2.22$, mean difference = 17.27; $P = 0.034$). Scenario 3 also had a shorter time to quasi-extinction than Scenario 4 (paired-t test: $t_{29} = 2.30$, mean difference = 17.00; $P = 0.029$).

Species varied substantially in their relative extinction risk as a result of population growth rate and environmental variance (Fig. 4). Models became essentially deterministic at low and high values of μ (Lande and Orzack 1988), and across species, μ explained the greatest variation in extinction risk (Fig. 5). When μ was < -0.06 , 200-year quasi-extinction risk was consistently $> 90\%$ across scenarios, while $\mu > -0.02$, coupled with low environmental variance resulted in no quasi-extinction risk at 200 years. Within species, extinction risk was greatest when environmental variance was highest, regardless of the amount of connectivity and area (Fig. 6), although across species, environmental variance explained little of the variation in extinction risk (Fig. 4). The most extinction-prone species (Spot-throat, Red-capped Forest Warbler, Tiny Greenbul, Usambara Thrush, and Striped-cheeked Greenbul) represented three feeding guilds (Table 1) and a range of population densities, although across species, population density explained a substantial amount of extinction risk (Fig. 5). Three of these five species were high elevation species (Table 1; all but Tiny Greenbul and Striped-cheeked Greenbul), which were constrained to the five highest elevation reserves. For these species, additional area added under Scenarios 3 and 4 did not improve population persistence because additional reserves were outside their elevational ranges.

Across species, the 200-year quasi-extinction risk decreased significantly with dispersal. For those species with moderately low μ estimates and extinction risk estimates not fixed at zero

or one across scenarios, 200-year quasi-extinction risk was 5.2% higher across scenarios when dispersal was disallowed (paired-t test: $t_{58} = 4.89$, $P < 0.001$). But we also found that extinction risk did not decrease linearly with added area and connectivity. Rather, for most species, extinction risk was the same or slightly higher under Scenario 3 relative to Scenario 2, even though Scenario 3 would include four additional corridors (Fig. 2). Although Scenario 3 would also add more area than Scenario 2, the additional habitat would be distributed among four small forest corridors rather than in one large block (all of the area added in Scenario 2 would be in the Nilo Nature Reserve Extension). Thus, Scenario 3 would increase dispersal of individuals to small forest tracts that are more extinction prone. Because dispersal also increases extinction risk through increased population synchrony, the benefits of dispersal might only be realized when there is sufficient habitat area or a particular habitat configuration (e.g., area added to fewer yet larger tracts). We suggest that the combined costs of dispersal in Scenario 3 likely outweighed the benefits. This is further supported by the substantially lower extinction risk seen in Scenario 4, which would add considerably more area than the other scenarios and which would connect all forest reserves into a single population.

Species-area relationships substantially underestimated future species losses relative to demographic analysis. Assuming z -values of 0.15 and 0.25, the exponential decay function estimated a future understory community size of 44.1 and 46.8 species, respectively, representing a projected 8.3 – 13.5% loss in understory bird biodiversity. By applying 200-year quasi-extinction risk from PVA (0.390) to the same starting community, we projected a final understory bird community size of 31 species, representing a projected 39.0% loss in species richness.

DISCUSSION

The East Usambara Mountains of Tanzania contain the highest levels of endemic and near-endemic species within the Eastern Arc biodiversity hotspot (Burgess et al. 2007b), which as a whole has the greatest numbers of endemic species per area among hotspots world-wide (Bishop and Myers 2005). Consequently, conservation of this fragmented tropical ecosystem is of global importance for slowing biodiversity loss and for providing lessons to guide conservation planning in similarly fragmented tropical forests. The reserve design scenarios under consideration in the EUM are ambitious and represent some of the best-case scenarios for conservation. Regardless, our results showed that even among relatively common understory bird species, 200-year quasi-extinction risk was very high for some species under the most protective scenario. Extinction rates of rarer species not represented in this study are likely to be even higher.

High species richness argues for protection of biodiversity hotspots and other high-priority conservation areas; however, our demographic analysis in one such hotspot demonstrates that a significant extinction debt is still to be paid (Tilman et al. 1994). Although slight changes in species richness metrics through time hint at dynamic faunal relaxation (Diamond 1972, O'Connell et al. 1998, Ferraz et al. 2003), demographic analyses provide a clearer insight into the extinction processes that are ongoing and pervasive in the EUM. That biodiversity hotspots like the Eastern Arc were selected in part based on the criterion of extensive habitat loss (Bishop and Myers 2005) means that many populations in these areas may be on a sharp extinction trajectory even if remaining habitat is protected. Species-area curves previously used to project species extinctions in biodiversity hotspots estimated that 18% of species in those areas would be lost within 100 years even if all the remaining area within these hotspots are protected (Pimm and

Raven 2000b). Demographic analyses in the EUM confirm that species will continue to be lost even if all remaining habitat is protected, but show that losses may be even higher than previously estimated, with an average 100-year quasi-extinction risk ranging from 20 – 31% depending on environmental variance. Thus, reversing the extinction process in highly fragmented and relatively small biodiversity hotspots like the Eastern Arc will require more than simply protecting remaining habitat.

Although the reserve scenarios did not eliminate extinction risk, an increase in reserve area and connectivity had the important benefit of delaying extinction for most species, providing a greater window of opportunity for implementing conservation strategies. Population viability analyses across 14 species showed that the most protective of the reserve options would delay 50% quasi-extinction risk by an average of three decades. For some species, 50% quasi-extinction risk was delayed by as many as 150 years in the most protected reserve network, relative to the status quo. In our models, these benefits derived from increasing initial population size due to larger reserve area and from dispersal. Even more important for determining extinction risk, however, was variation in population growth rate and environmental variance among species. These parameters set the shape and slope of extinction risk curves, which were only shifted to some degree by the effects of reserve planning. Thus, while an enhanced reserve network can improve population persistence, the magnitude of changes required to reverse the extinction trajectory for most species will also require substantial changes in population growth rate and environmental variance. Although we were not able to model future trends in vital rates, population growth rate and environmental variance could improve with larger and more-connected populations, especially in light of previous demographic analyses that have shown population growth rates of understory birds were greater (although still generally negative) on

large forest fragments relative to small (Korfanta chapter two). In that case, an enhanced reserve network might improve population persistence beyond our estimates. Population growth rates may also be increase through improvements to habitat quality such that existing reserves are no long population sinks. Indeed, several of the most extinction-prone species included in our analysis, such as the Spot-throat and Usambara Thrush, preferentially use primary or slightly disturbed forest in the East and West Usambara Mountains (Newmark et al. 2010). Thus, reducing forest disturbance may be particularly important in improving persistence of such species.

Among the most commonly advanced approaches to mitigate fragmentation effects is improved connectivity of otherwise isolated habitat remnants, which can promote demographic and genetic rescue effects, provide habitat for transient individuals, and facilitate juvenile dispersal, among other benefits (summarized by Crooks and Sanyayan 2006). However, few studies have documented the effects of corridors on community dynamics and, as a result, evidence for actual benefits of corridors is weak (Haddad et al. 2000). We found that dispersal was generally beneficial in lowering extinction risk across the understory bird community, but that its specific effect on each reserve scenario was sometimes negligible and not easily predicted. We suggest the variable effect of dispersal reflected a complex response to the benefits of demographic rescue effects versus the costs of population synchrony and movement of individuals to potential population sinks, a result that would not be easily predicted without the benefit of multi-site PVA. Our findings were consistent with other studies showing that dispersal ameliorates but does not eliminate extinction risk in fragmented landscapes (Taylor et al. 1993, Reed 2004, Sandercock et al. 2005). Further, our results demonstrated variable dispersal effects may arise simply through habitat configuration and changes to population

synchrony, which may be additive to the effects of increased disease transmission (e.g., Hess 1994, Grenfell and Harwood 1997, Daszak and Cunningham 1999), increased predation rates (Ambuel and Temple 1983), or synchronized catastrophes (Armbruster and Lande 1993) that are often cited as the costs of dispersal. A similar demographic cost of dispersal was found in models of arboreal marsupials, which showed decreased population persistence when small populations were connected by dispersal (Lindenmayer et al. 2002). Connectivity conservation places great emphasis on restoring functional connectivity to promote movement of individuals through the landscape (Taylor et al. 1993), a feature we incorporated in our model through wide (1 km) corridors. Our results provide evidence that community viability may indeed improve with functional connectivity, but that in some cases even very wide corridors may still present bottlenecks for minimally dispersing species, such that the corridors provide no net benefit to reserve-wide population persistence. Reserve designs should, therefore, incorporate connectivity thoughtfully and selectively. In practice, that may mean prioritizing corridors that connect large reserves and carefully modeling the demographic consequences of promoting dispersal from large reserves to smaller corridors.

To our knowledge, this is the first application of count-based PVA for multiple-species reserve design, and as such, provides an opportunity for comparison with traditional approaches. In lieu of population viability analysis, which is prohibitively data-intensive for most species of conservation concern, reserve areas are prioritized and evaluated through species richness metrics and the capacity of those reserves to conserve species in the long-term is evaluated through species-area relationships (Cabeza and Moilanen 2001, Lindenmayer et al. 2002). However, we found that even when accounting for time lags in biodiversity loss (Rosenzweig 1995, O'Connell et al. 1998, Ferraz et al. 2003), post-fragmentation species richness was

substantially overestimated relative to projections from PVA. That greater species loss was predicted from PVA was not surprising given the incorporation of environmental stochasticity and declining population trends, which combine to diminish dynamic population persistence. However, the magnitude of difference between demographic and species-area approaches suggests that projections of species losses from even well-protected biodiversity hotspots may be even greater than previously anticipated (Pimm and Raven 2000). Further, demographic analysis revealed a wide-range of species-specific extinction risk not easily predicted from life history or ecological correlates such as feeding guild or population density. As a result, reserve design in the EUM may better target the particular needs of the most-extinction prone species.

Management implications

With a growing human population and attendant land conversion to agricultural uses, the EUM is predicted to have among the highest rates of future species extinctions of any biodiversity hotspot (O'Connell et al. 1998). In response to that challenge, the Tanzanian government has begun to upgrade the protective status of many forest reserves and to gazette new reserves (Burgess et al. 2007b). Our results suggest at least five lessons for land managers and policy makers interested in conserving tropical forest biodiversity:

- 1) When possible, reserve design should be based on the population processes of multiple species. Even within the same understory bird community, we found substantial variation in extinction risk under the four reserve scenarios. Had we focused on only the most fragmentation-sensitive species, such as Spot-throat, we might have concluded that the costs of increasing EUM reserves were not warranted given the species' high extinction risk. Similarly, a focus on Tambourine Dove would have over-estimated community resilience to fragmentation effects.

2) Increasing connectivity, particularly among large reserves, can improve population persistence across the avian community. By contrast, encouraging dispersal to relatively small forest reserves or corridors may not confer the same benefit.

3) Increasing connectivity, coupled with small increases in habitat quantity, might not be sufficient to conserve most species over the long-term. Substantially negative growth rates will eventually precipitate extinctions, regardless of connectivity. Additional conservation strategies might also need to target habitat quality as a way to boost population growth rates.

4) The short extinction horizon for some species suggests that corridors and additional habitat should be actively re-vegetated rather than waiting for passive re-growth.

5) Long-term conservation of some species may require a broad geographic perspective. Particularly for high-elevation species at the edge of their distributional range, local extinctions are likely in the EUM regardless of increasing connectivity. For those species, conservation of the higher elevation habitat in the West Usambara Mountains and in other Eastern Arc mountains may be critical for long-term persistence. Conserving multiple, geographically distinct populations would minimize the risks associated with population synchrony and would be a wise long-term strategy in the face of unknown climate change effects.

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TABLES AND FIGURES

Table 1. Names, feeding guilds, estimated population density (Stuart 1991), approximate elevation range used to determine suitability of proposed reserves/corridors (Fig. 2), and population growth rate (λ) for 14 study species.

Family	Scientific name	Common name	Feeding guild	Density (indiv/ 100 ha)	Elevation range category	λ (SE)
Columbidae (pigeons and doves)	<i>Turtur tymanistria</i>	Tambourine Dove	Granivore	20	Low-high	1.055 (0.017)
Timaliidae (babblers)	<i>Trichastoma rufipennis</i>	Pale-breasted Illadopsis	Terrestrial insectivore	130	Low-high	0.996 (0.014)
Pycnonotiidae (bulbuls)	<i>Andropadus milanjensis</i>	Striped-cheeked Greenbul	Frugivore	120	Low-high	0.960 (0.007)
	<i>Phyllastrephus debilis</i>	Tiny Greenbul	Insect gleaner	50	Low-high	0.954 (0.014)
	<i>Phyllastrephus placidus</i>	Cabanis's Greenbul	Insect gleaner	140	Mid-high	0.984 (0.010)
	<i>Phyllastrephus flavostriatus</i>	Yellow-streaked Greenbul	Insect gleaner	230	Low-high	0.997 (0.009)
Turdidae (thrushes)	<i>Alethe fuelleborni</i>	White-chested Alethe	Insect gleaner	180	Mid-high	1.005 (0.008)

	<i>Modulatrix stictigula</i>	Spot Throat	Insect gleaner	220	High	0.835 (0.047)
	<i>Sheppardia sharpei</i>	Sharpe's Akalat	Insect gleaner	140	Mid-high	0.998 (0.013)
	<i>Turdus abyssinica</i>	Usambara Thrush	Insect gleaner	80	High	0.967 (0.016)
	<i>Turdus gurneyi</i>	Orange Ground Thrush	Insect gleaner	80	Mid-high	0.979 (0.011)
Sylviidae (warblers)	<i>Orthotomus metopias</i>	Red-capped Forest Warbler	Insect gleaner	80	High	0.879 (0.047)
	<i>Phylloscopus ruficapilla</i>	Yellow-throated Woodland Warbler	Insect glenaer	40	High	0.987 (0.014)
Muscicapidae (flycatchers)	<i>Batis mixta</i>	Forest Batis	Sallier	140	Low-high	0.980 (0.013)

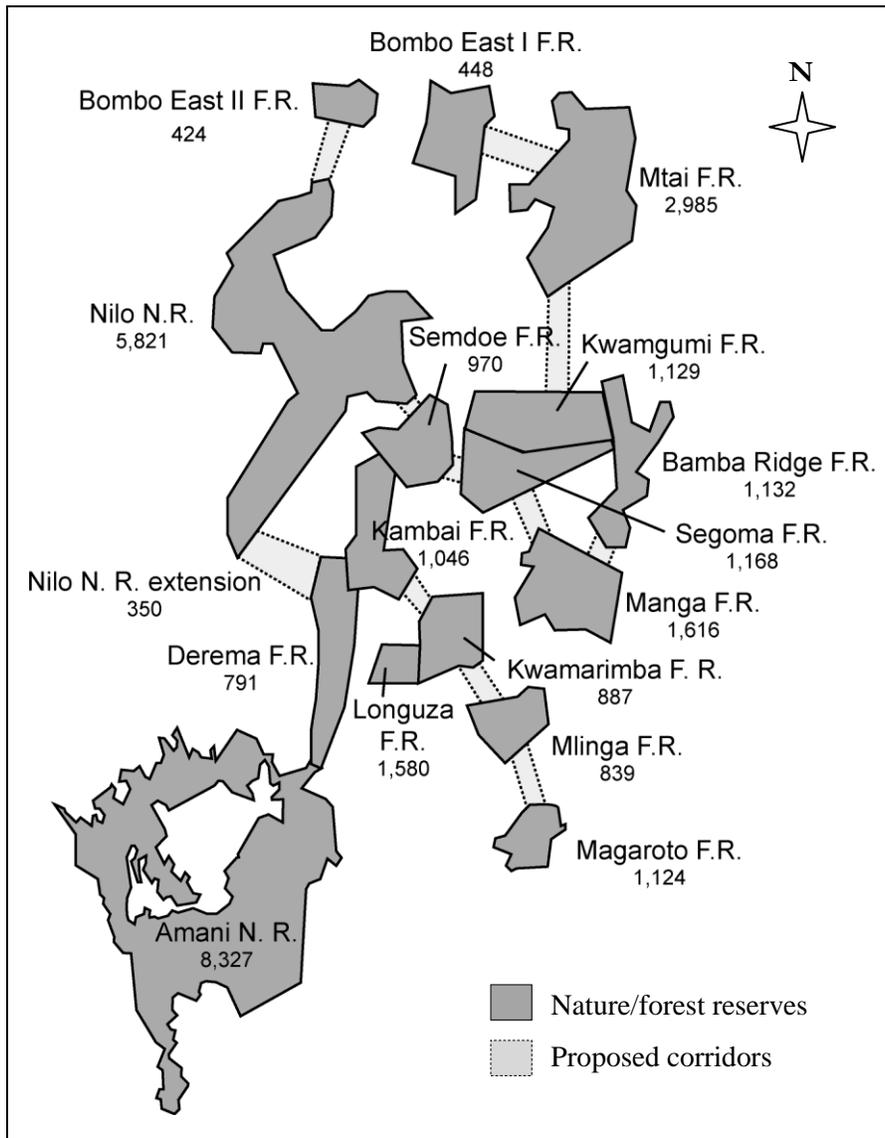


Figure 1. Map of existing forest and nature reserves in the East Usambara Mountains, Tanzania, including approximate areas (ha; Johansson 1994) and linkages via proposed corridors (map not drawn to scale).

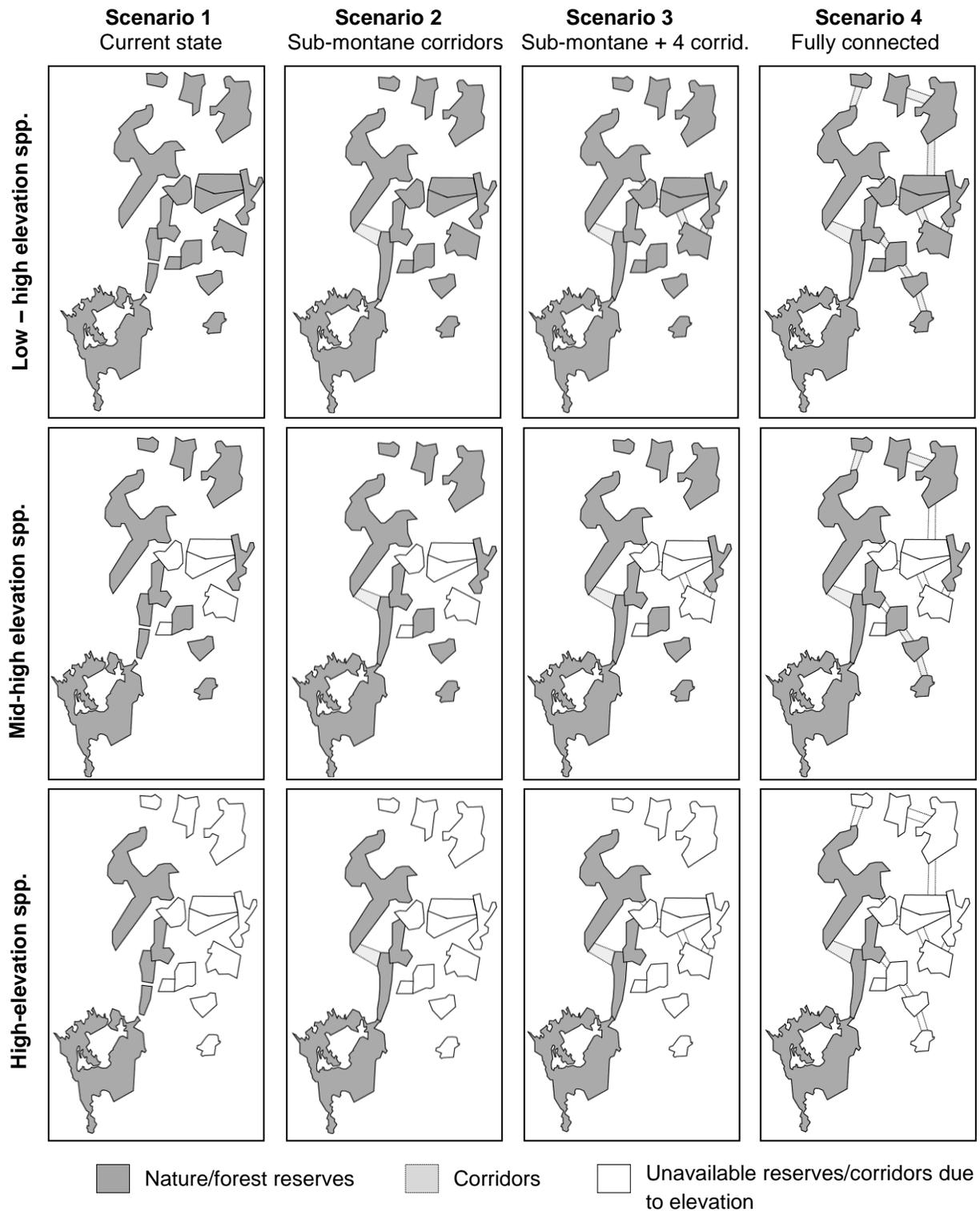


Figure 2. Maps showing protected reserves and corridors under four potential reserve networks ranging from the status quo (Scenario 1) to fully connected (Scenario 4). Variation within scenarios represents the locations available to three groups of species based on elevation range constraints. Reserve/corridor availability was determined from species' elevational ranges, with reserve/corridors that did not overlap a species elevational range classified as unavailable.

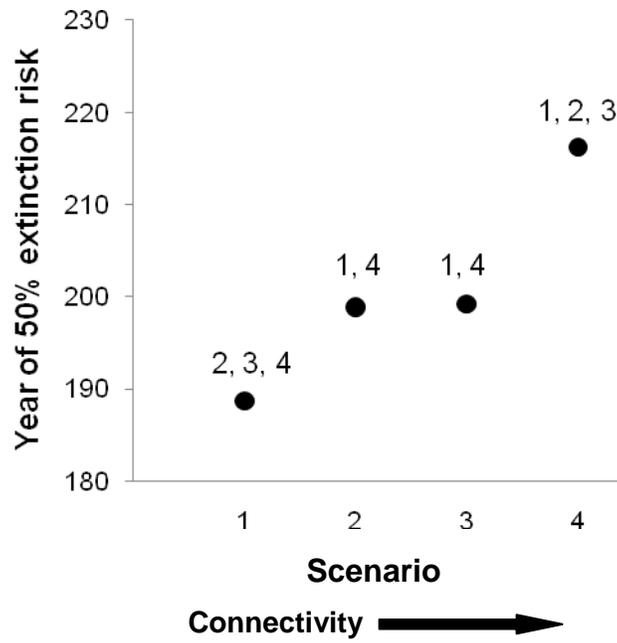


Figure 3. Mean time to 50% quasi-extinction risk averaged across species. Numbers above each point denote the reserve scenarios for which paired t-tests were different ($P < 0.05$; test statistics provided in the text).

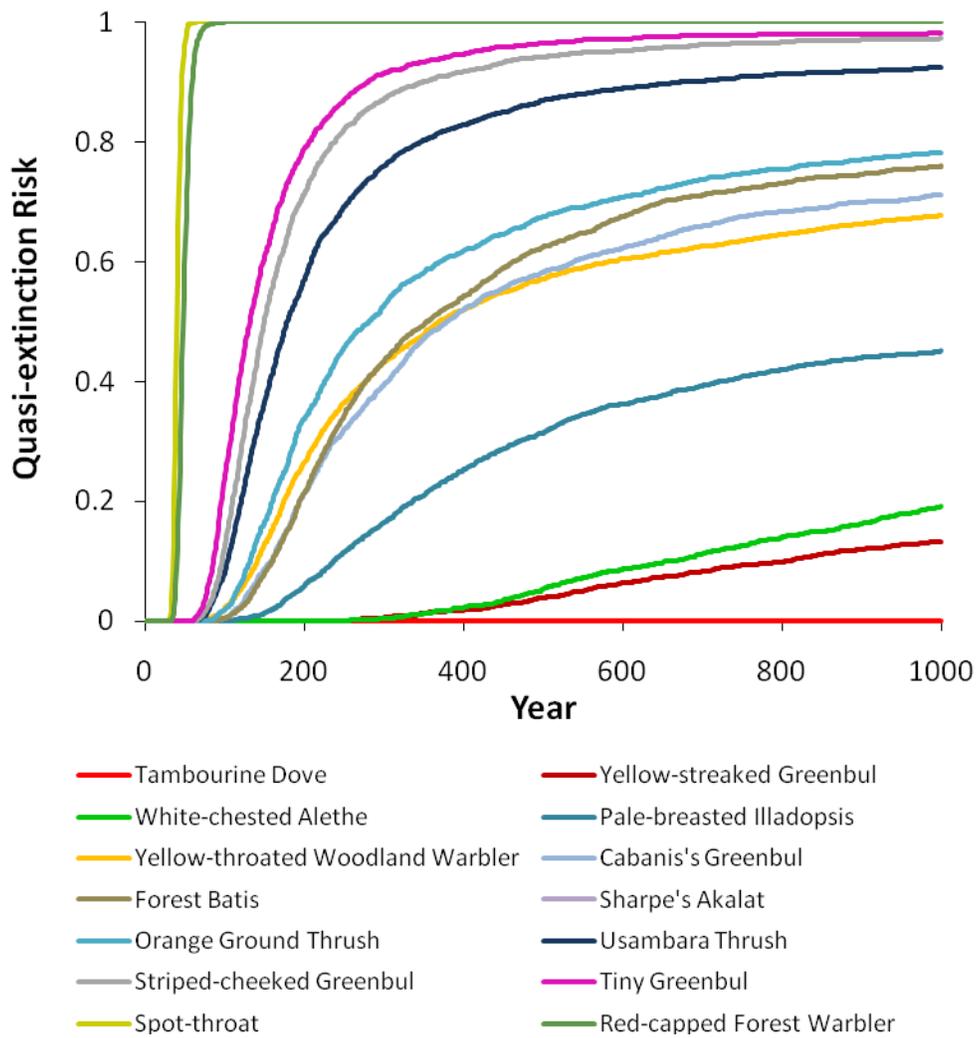


Figure 4. Cumulative distribution functions showing quasi-extinction probability for each species under the most protective scenario and assuming low environmental variance.

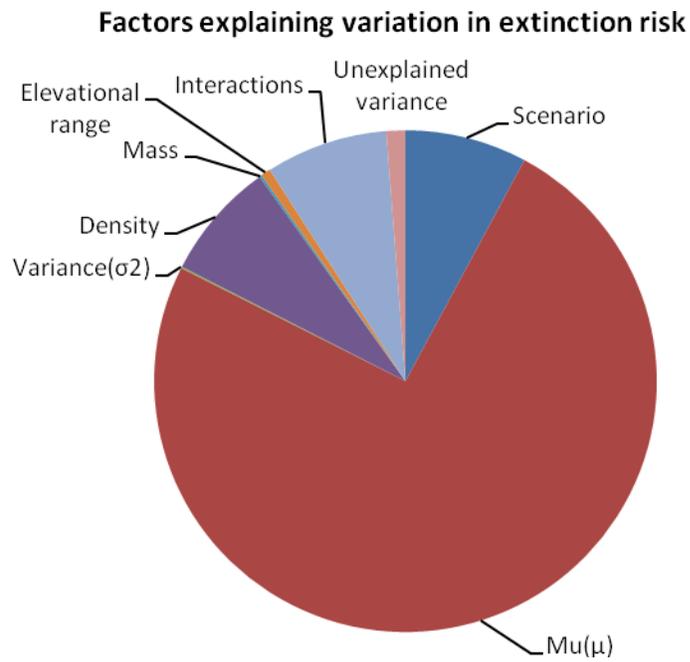
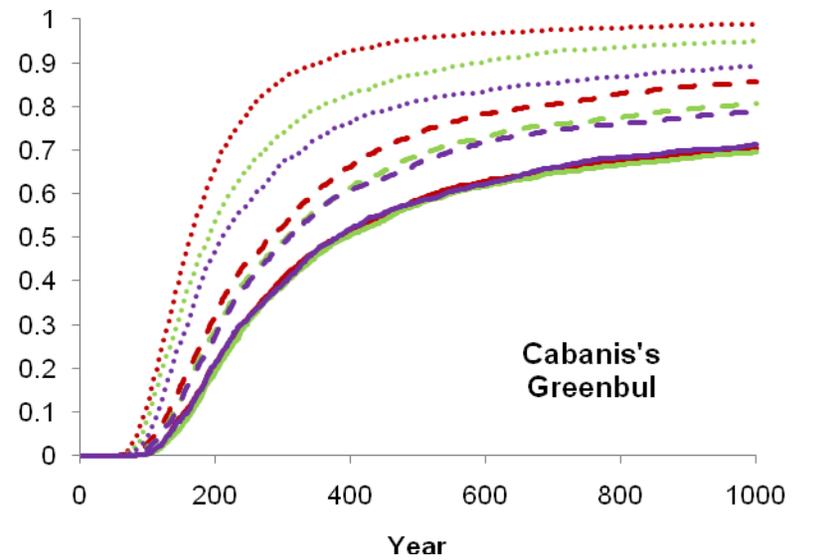
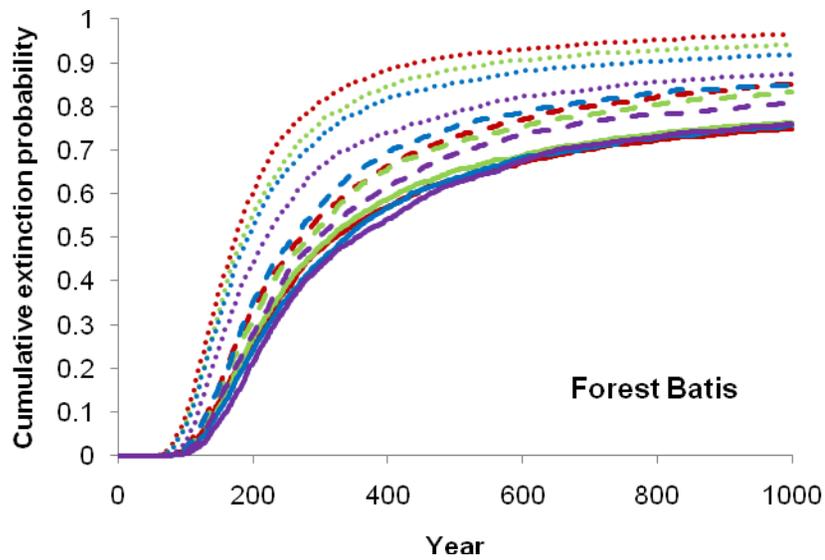
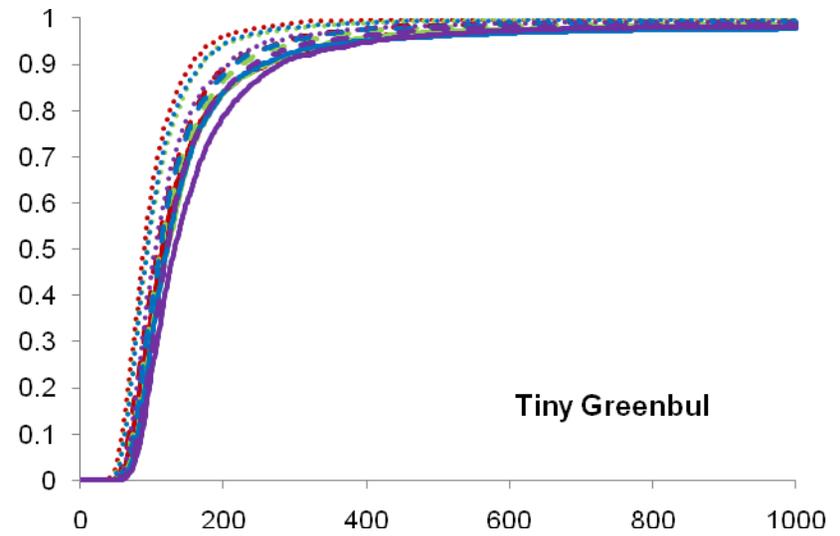
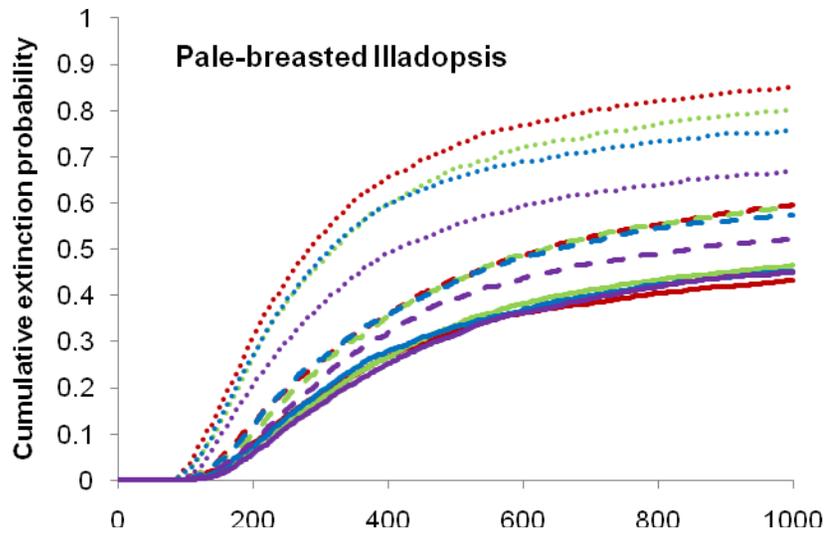
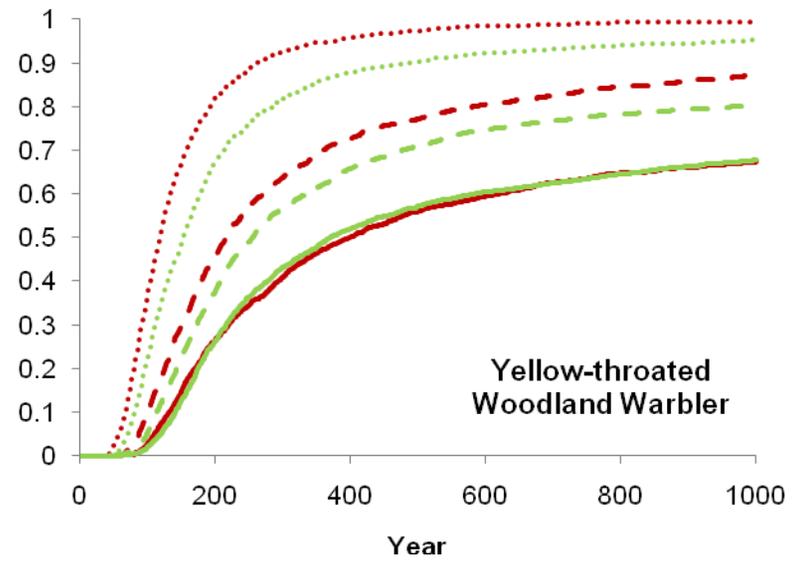
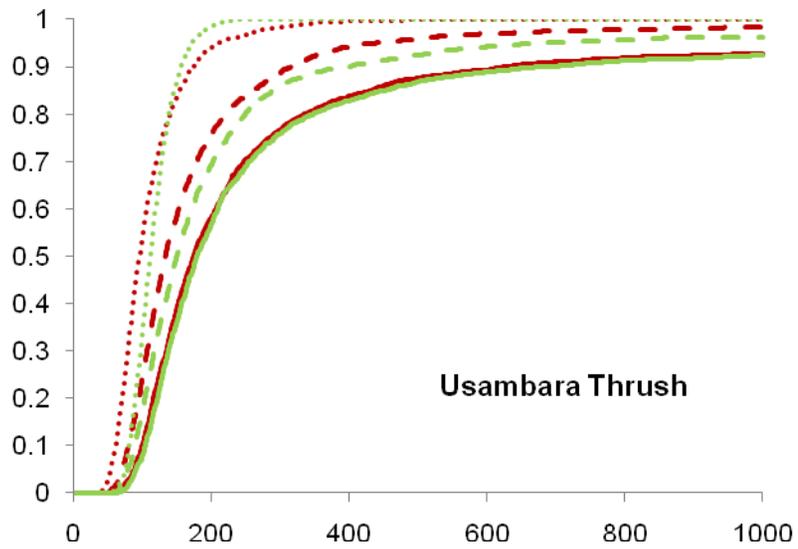
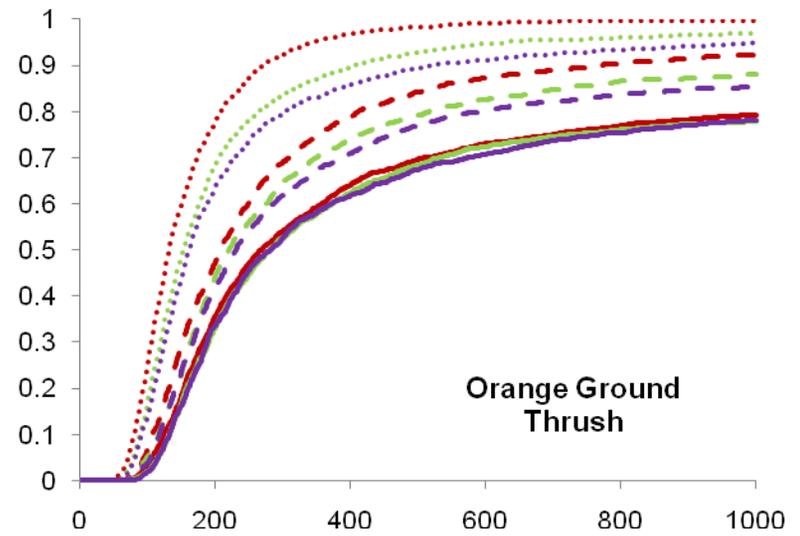
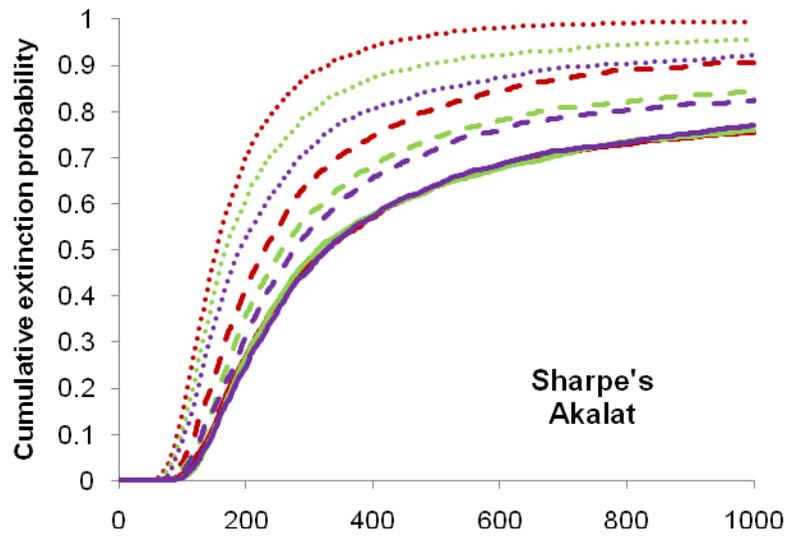
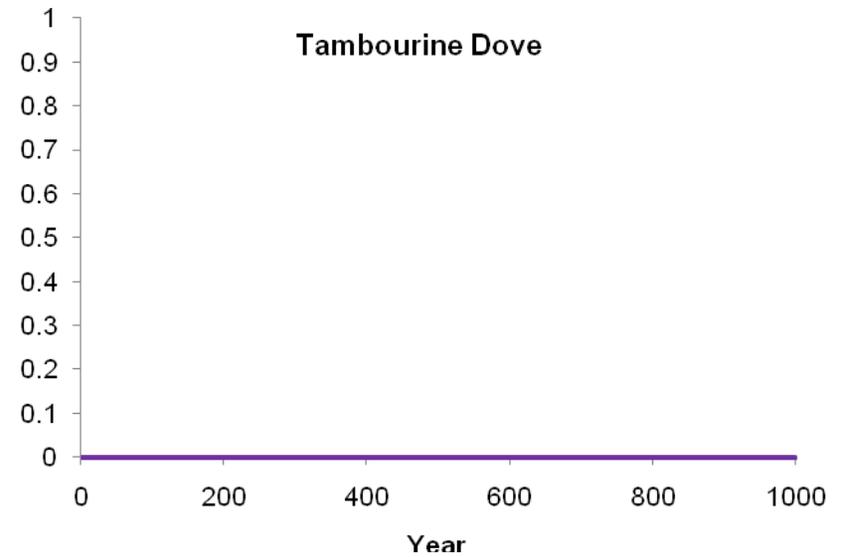
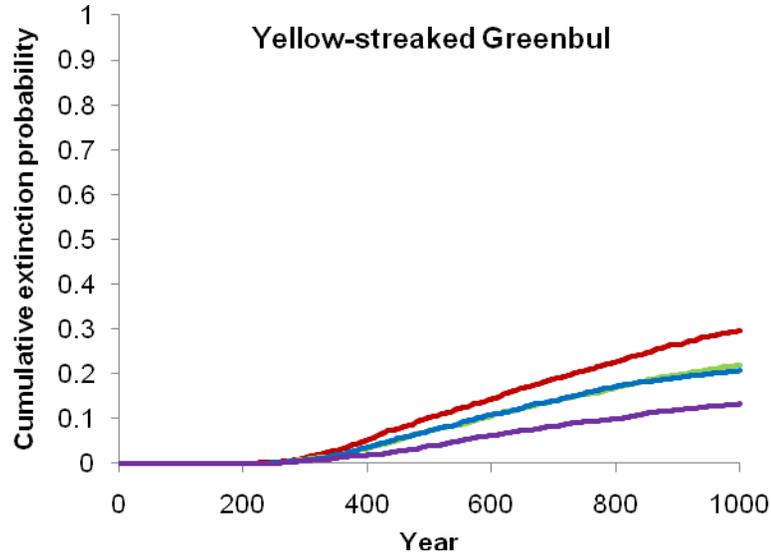
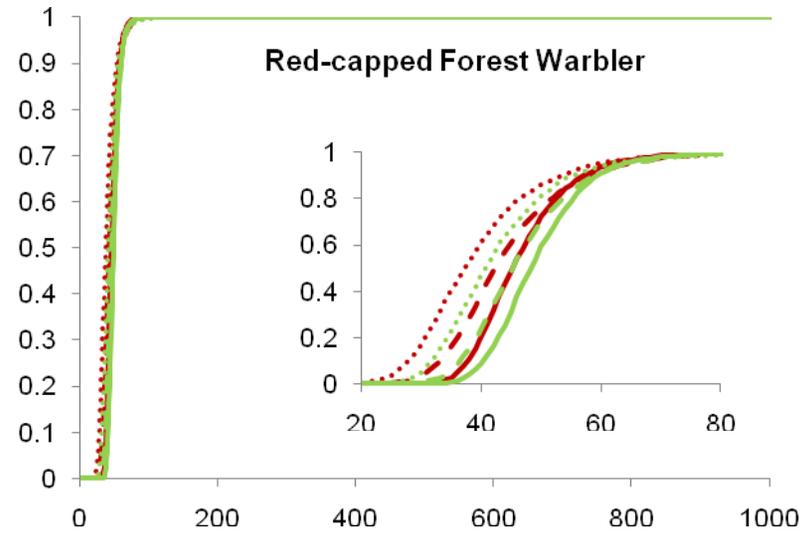
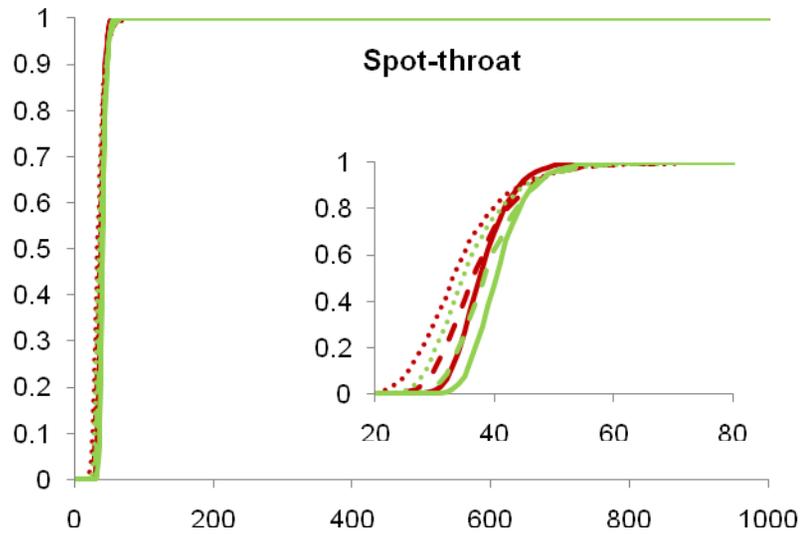


Figure 5. Proportion of ANOVA variance (sum of squares) explained by a range of factors. “Interactions” includes the sum of all possible two-way interactions among variables.







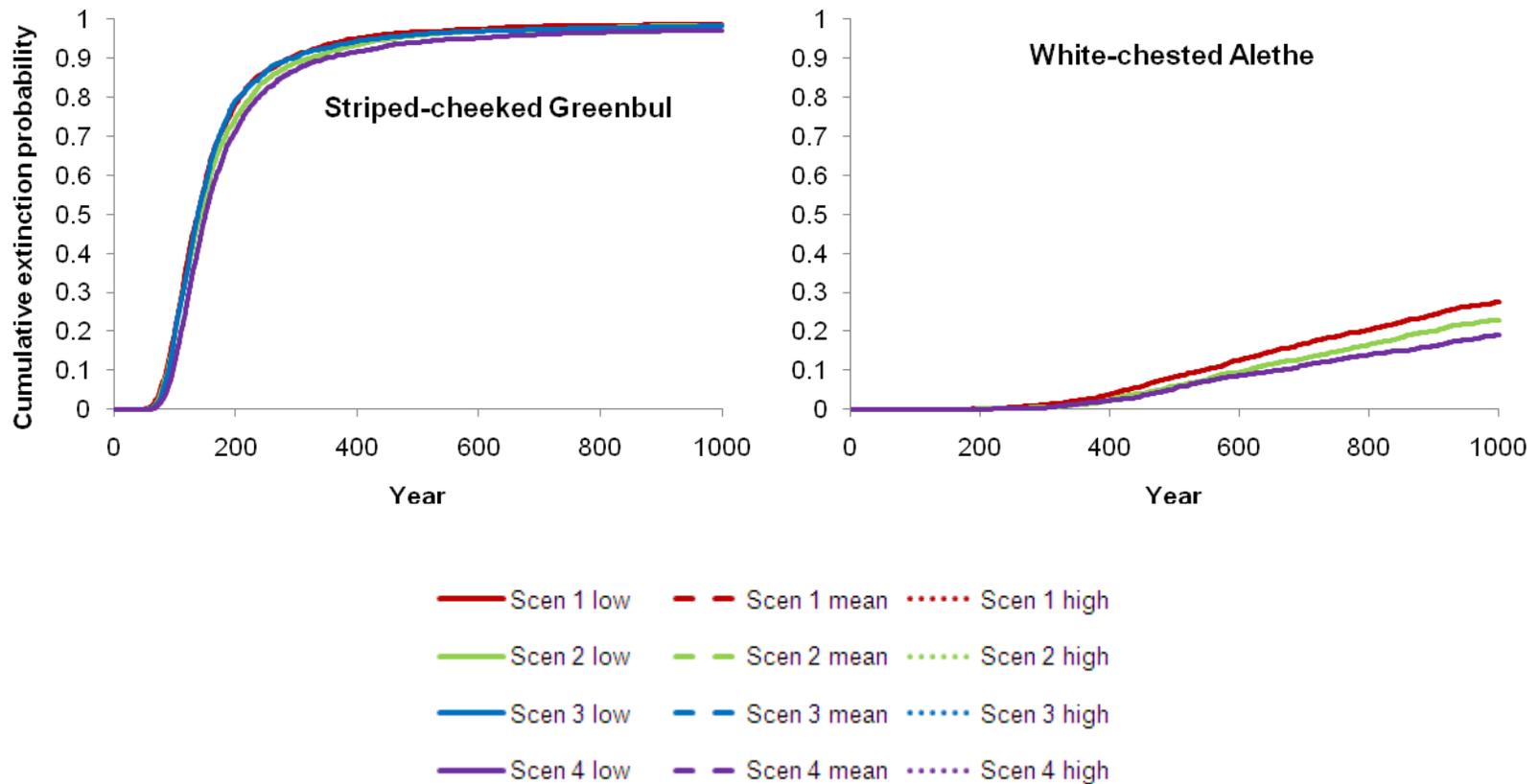


Figure 6. Cumulative distribution functions (CDF) showing 1000-year extinction risk for each species. Curves represent Scenarios 1-4 (from smallest and least connected to largest and most connected) and a range of environmental variance (σ^2) estimates (low, mean, and high), except for those species for which we had species-specific σ^2 estimates (Yellow-streaked Greenbul, Tambourine Dove, Striped-cheeked Greenbul, White-chested Alethe). Across species, the lowest extinction risk resulted from greater connectivity and area, combined with low σ^2 .

CHAPTER FIVE

Discussion

The tropics contain an estimated two-thirds of all species (Pimm and Raven 2000a), many of which are found in the humid tropical forests that have already undergone roughly 50% habitat loss (Skole and Tucker 1993) and are predicted to have high deforestation rates in the future (Balmford et al. 2001). Local and range-wide extinctions of avian species thus far represent the most fragmentation-sensitive species of the community, but a well-documented time lag between habitat loss and full relaxation to a new equilibrium species number means that additional extinctions are on the horizon (Tilman et al. 1994, O'Connell et al. 1998, Ferraz et al. 2003). A key question in conservation science is how we can best predict which species are most vulnerable to fragmentation effects and how rapidly species losses will occur so that we might better conserve them. Traditional community-level, species-richness analyses provide a framework for understanding fragmentation effects by predicting the diversity of post-fragmentation communities (O'Connell et al. 1998). However, the constituent species within the community are not readily identified from that approach (Laurance et al. 2008). Life-history correlates narrow the predictions of species-area relationships by relating extinction risk to easily-observed qualities such as body size, dispersal ability, or feeding guild (reviewed by Reed 1999, Henle et al. 2004, Sodhi et al. 2004, Saether et al. 2005). Because life-history traits interact in complex ways to alter extinction risk across species, such an approach is most valuable for explaining broad trends in extinction risk rather than for predicting species-specific extinction risk (Pimm et al. 1988, Sodhi et al. 2004). Demographic analyses can add to both of these approaches by quantifying the underlying population processes that drive extinction risk, allowing for a more direct assessment of fragmentation effects prior to extinction. Estimation of

vital rates also facilitates population viability analysis, with which we can model future persistence across a range of management scenarios (Nicholson and Possingham 2006).

In Chapter 2, I used mark-recapture approaches to estimate fragmentation effects on apparent survival, population growth rate, recruitment, and seniority across 22 species. To my knowledge, this is the first study to estimate fragmentation effects on survival across a suite of avian species (but see Karr 1990 for a multi-species analysis of variable survival rates on islands versus mainland). Although there was some variation in the magnitude and even direction of fragmentation effects, results showed a significant and negative effect of fragmentation on apparent survival across species. Apparent survival was also lower on small fragments relative to large, and was generally < 1 for most species. Because the effect of fragmentation on recruitment was inconsistent and not significantly different between small and large forest fragments, I ascribed generally depressed population growth rates to lower survival. These results are significant because most prior demographic work for birds has focused on the effects of fragmentation on nest success (Lampila et al. 2005b). Although such work has shown significant fragmentation effects on productivity parameters (Stephens et al. 2003), these rates may be less important than survival for long-lived tropical bird species (the average maximum age of species in this study was 11.8 years) (Saether and Bakke 2000b). Also, most demographic studies focus on a single species selected *a priori* because of their fragmentation sensitivity (Lampila et al. 2005b). Only through analysis of a cross-section of the understory bird community was I able to identify survival as the dominant demographic driver of population declines, although for some species, both depressed survival and recruitment combined to create significant population declines. For most species, however, my finding of depressed survival suggested that minimizing adult mortality would be the most effective way to slow population

declines and avert additional extinctions. Future work could better characterize the impacts of habitat fragmentation on important nest predators such as., snakes, raptors, and rodents).

The persistent demographic consequences of habitat fragmentation demonstrated in Chapter 2 suggested elevated extinction risk for even common members of the understory bird community. Future population trajectories are, however, determined not only by population growth rate (λ), but also by demographic and environmental stochasticity that cause variation around λ (Lande 1998, Lande et al. 2003). In Chapter 3, I used count-based population viability analysis (PVA) (Dennis et al. 1991, Morris and Doak 2002) to model the probability of future population persistence as a function of λ and environmental variance for eight species representing a range of life-history attributes and fragmentation responses. The first key finding of this chapter was that a relatively simple count-based PVA accurately predicted extinction risk for dispersal-limited species. Although the validity of PVA has been challenged when data are limited (O'Connell et al. 1998, e.g., Coulson et al. 2001, Ellner et al. 2002, Sandercock and Beissinger 2002), historical validation showed strong congruence between predicted and observed extinctions, confirming PVA as a potentially powerful tool for evaluating management options (O'Connell et al. 1998, Morris et al. 2002). That PVA overestimated extinction risk for moderately dispersing species is itself revealing because it highlights the importance of dispersal in counteracting extinction risk associated with habitat fragmentation (Gascon et al. 1999, Sekercioglu et al. 2002, Van Houtan et al. 2007). For the remaining species, I found a high probability of quasi-extinction within 100 years for all species on small forest fragments. Of greater conservation concern was the finding that two of the species also had high extinction risk on medium and large-size forest fragments as well. These results have important conservation implications and suggest that simply protecting the remaining large forest tracts in the East

Usambara Mountains will not be sufficient to reverse the extinction debt from past habitat loss (Tilman et al. 1994, Pimm and Raven 2000c). Finally, this chapter provided greater insight into the parameters that most affect extinction risk in a tropical avian community. Across species, I found that wide variation in extinction risk was driven in part by species-specific environmental variance that amplified the effects of population growth rate on viability (Lande and Orzack 1988, Melbourne and Hastings 2008). Although ecological theory predicts that habitat fragmentation may increase environmental variance through both abiotic and biotic drivers (Armbruster and Lande 1993, Woodroffe and Ginsberg 1998, Laurance et al. 2002), this was among the first studies to validate that theory by showing higher environmental variance on small forest fragments. This finding suggests that assumptions about environmental variance must be made carefully when parameterizing PVAs and that population-specific estimates are ideal when possible (Saether et al. 2005).

Because analyses from Chapter 3 showed high extinction risk for some species on large forest fragments, in Chapter 4 I used a PVA model to assess whether increased connectivity among existing protected areas could lessen extinction risk across the understory bird community in the East Usambara Mountains. PVA is recognized as a potentially powerful tool for evaluating a range of management options (Lindenmayer et al. 2002, Morris and Doak 2002), but its full utility has rarely been realized to guide reserve design in tropical ecosystems. Although the reserve design scenarios under consideration in the EUM were ambitious and represented some of the best-case scenarios for conservation, I found that even for some relatively common understory bird species extinction risk was very high under the most protective scenario. Nonetheless, an increase in reserve area and connectivity had the important benefit of delaying extinction for most species, providing a greater window of opportunity for

implementing additional conservation activities. Given the findings of Chapter 3, which showed that dispersal ameliorated extinction risk in some species, I also compared PVA models with and without dispersal effects to test assumptions about the benefits of promoting population connectivity through reserve design (summarized by Crooks and Sanyayan 2006). My results confirmed that dispersal was generally, but not always, beneficial in lowering extinction risk across the understory bird community (Lindenmayer et al. 2002). Specifically, promoting dispersal to small forest reserves did little to reduce reserve-wide extinction risk, a finding consistent with other taxa and systems (e.g., Lindenmayer and Lacy 1995). This result suggests that reserve planning should incorporate connectivity selectively, particularly by prioritizing corridors that connect large reserves. Finally, this was the first application of count-based PVA for multiple-species reserve design, and as such, provided an opportunity for comparison with traditional species richness approaches typically used to assess habitat fragmentation effects. Relative to demographic analysis, I found that species-area curves generated from species richness measures substantially overestimated post-fragmentation species richness. Thus, a demographic approach to understanding habitat fragmentation effects demonstrated more severe and extinction risk across a broader range of species than previously appreciated from species-area relationships. Together, these results suggest that future biodiversity loss in even highly protected biodiversity hotspots may be even greater than previously anticipated (Pimm and Raven 2000).

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