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Sufficient versus optimal climatic stability during the Late Quaternary: using environmental quality to guide phylogeographic inferences in a Neotropical montane system

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Quaternary climatic oscillations affected species distributions worldwide, creating cycles of connectivity and isolation that impacted population demography and promoted lineage divergence. These effects have been well studied in temperate regions. Taxa inhabiting mesic montane habitats in tropical ecosystems show high levels of endemism and diversification in the distinct mountain ranges they inhabit; such a pattern has commonly been ascribed to past climatic oscillations, but few phylogeographic studies have tested this hypothesis. Here, we combine ecological niche models of species distributions with molecular data to study phylogeographic patterns in two rodents endemic to the highlands of Costa Rica and western Panama (*Reithrodontomys creper* and *Nephelomys devius*). In so doing, we apply a novel approach that incorporates a basic ecological principle: the expected positive relationship between environmental suitability and population abundance. Specifically, we use niche models to predict potential patterns of population connectivity and stability of different suitability levels during climatic extremes of the last glacial–interglacial cycle; we then test these predictions with population genetic analyses of a mitochondrial and a nuclear marker. The detailed predictions arising from the different levels of suitability were moderately to highly congruent with the molecular data depending on the species. Overall, results suggest that in these tropical montane ecosystems, cycles of population connectivity and isolation followed a pattern opposite to that typically described for temperate or lowland tropical ecosystems: namely, higher connectivity during the colder glacials, with isolation in montane refugia during the interglacials, including today. Nevertheless, the individualistic patterns for each species indicate a potentially wide gamut of phylogeographic histories reflecting particularities of their niches. Taken together, this study illustrates how phylogeographic inferences may benefit from niche model outputs that provide more detailed predictions of connectivity and finer characterizations of potential refugia through time.

Las oscilaciones climáticas del Cuaternario afectaron la distribución de las especies a lo largo del planeta, causando ciclos de conectividad y aislamiento, con impactos en la demografía poblacional y divergencia de los linajes. Estos efectos han sido ampliamente estudiados en regiones templadas; se sabe poco de los ecosistemas tropicales, en particular respecto a los grupos taxonómicos de hábitats montanos húmedos. Estos taxa presentan altos niveles de endemismo y una gran divergencia entre las distintas cadenas montañosas que habitan. Estos patrones han sido adjudicados a oscilaciones climáticas del pasado; sin embargo, pocos estudios filogeográficos han puesto a prueba esta hipótesis. En este trabajo, combinamos modelos de nicho ecológico y distribución de especies con datos moleculares, analizando los patrones filogeográficos de dos roedores endémicos a las tierras altas de Costa Rica y el oeste de Panamá (*Reithrodontomys creper* y *Nephelomys devius*). En especial, abordamos el problema aplicando un nuevo procedimiento que incorpora un principio ecológico básico: la relación positiva esperada entre la idoneidad ambiental y el tamaño poblacional y/ tamaño poblacional o abundancia. Específicamente, utilizamos modelos de nicho ecológico que predicen los patrones de conectividad y estabilidad poblacional esperados bajo distintos niveles de idoneidad ambiental, durante extremos climáticos del último ciclo glacial. Luego ponemos a prueba las predicciones de los modelos mediante análisis de genética poblacional, utilizando un marcador mitocondrial y uno nuclear. Las predicciones específicas derivadas de los distintos niveles de idoneidad ambiental fueron apoyadas por los datos moleculares de manera moderada a alta dependiendo de la especie. En general, los resultados sugieren que en ecosistemas montañosos tropicales, los ciclos de conectividad y aislamiento poblacional siguieron un patrón opuesto al típicamente descrito para ecosistemas templados o para bosques tropicales de tierras bajas. Este patrón opuesto consiste de una mayor conectividad poblacional durante los fríos glaciales, seguido de un aislamiento en refugios montañosos durante los cálidos interglaciales, incluido el actual. No obstante, la naturaleza de los patrones obtenidos para cada roedor, indica una gama potencialmente amplia en cuanto a historias filogeográficas que reflejan las particularidades del nicho ecológico de cada especie. En resumen, este estudio muestra cómo las inferencias filogeográficas se pueden beneficiar de modelos de nicho ecológico que proporcionen predicciones más detalladas en cuanto a la conectividad potencial entre poblaciones, así como una caracterización más fina de refugios a través del tiempo.

Key words: Costa Rica, divergence, glaciation, Neotropical, niche model, Panama, refugia, sampling bias, sky islands, species distribution model

Climatic fluctuations of the Quaternary are considered important drivers of biodiversity patterns globally (Hewitt 2000; Lomolino et al. 2006; Stewart et al. 2010). This period was characterized by cycles of long-lasting glacials (~100,000 years; when environmental conditions were cooler and usually drier), punctuated by much shorter interglacials (~10–15,000 years; which were warmer and usually wetter), such as the one being experienced today (Webb and Bartlein 1992; Rutherford and D'Hondt 2000; Liu et al. 2008). By affecting the distribution and availability of particular environments, these cycles influenced the population demography of ancestral biotas, strongly contributing to the genetic patterns observed today, including those regarding lineage divergence (Lister and Hewitt 2004; Colwell and Rangel 2010; Stewart et al. 2010).

The effects of these climatic changes have been studied mostly in northern latitudes, where the expansion and contraction of ice sheets are correlated with major shifts in species distributions along altitudinal and latitudinal gradients, presumably as species tracked suitable environments and biotic resources (Brown 1971; Knowles 2000; Davis and Shaw 2001). Generally speaking, glacial phases in those regions resulted in distributional displacements toward lower latitudes and elevations—commonly referred to as "geographic or Pleistocene refugia"—from which the species recolonized during the warmer interglacials, as glaciers receded (Hewitt 2004; Waltari et al. 2007). This pattern is best exemplified by species associated with mid-temperate habitats today (e.g., deciduous forests and deserts), whose current patterns of genetic structure and divergence have been linked to severe range contraction and isolation occurring during glacial phases (Knowles 2000; Jezkova et al. 2011; Wilson and Pitts 2012). Species associated with colder environments at these and higher latitudes (e.g., those now occupying polar habitats or temperate mountain peaks) also experienced range displacement toward lower latitudes during the interglacials. Nevertheless, it has been proposed that such movements allowed for the colonization of previously inaccessible or unsuitable habitats (e.g., adjacent mountain peaks and intervening lowlands—Brown 1971; Patterson 1982; Good and Sullivan 2001). This process would result in demographic consequences opposite to those mentioned above; indeed, for such species, available genetic data support geographic expansions during cold glacial phases and retraction to polar or highland refugia during interglacials (Galbreath et al. 2009, 2010; Stewart et al. 2010). Distinguishing between such demographic scenarios when studying the effects of past climatic fluctuations on lineage divergence is crucial, given the disparity in time duration between glacial and interglacial phases, and hence, on the expected duration of isolation among populations.

Quaternary climatic oscillations also affected tropical latitudes, but their biogeographic effects on such biotas are less understood (Carnaval and Bates 2007; Amaro et al. 2012; Ramírez-Barahona and Eguiarte 2013). Here, glacial phases were also characterized by decreases in temperature (e.g., 4–10°C—Colinvaux et al. 1996; Hooghiemstra and Van der Hammen 2004; Marchant et al. 2009), leading to the expectation of concomitant shifts in species distributions. Recent phylogeographic studies of tropical rainforest taxa have inferred patterns of population connectivity and isolation analogous to those gathered for temperate taxa (i.e., expansions during interglacials—Hugall et al. 2002; Byrne 2008; Carnaval et al. 2009); nevertheless, several other studies suggest that such climatic fluctuations had little effect on species-level divergence (Rull 2011; Poelchau and Hamrick 2013; Ortego et al. 2015). Most notably, however, very little such research has been conducted on montane tropical biotas associated with cool, mesic conditions (Robin et al. 2010; Gutiérrez-Pinto et al. 2012; Demos et al. 2014), where cycles of isolation and connectivity are expected to have followed a pattern opposite to that of the lowland rainforests (equivalent to that of taxa inhabiting polar latitudes or temperate montane peaks—Amaro et al. 2012; Ramírez-Barahona and Eguiarte 2014; Paz et al. 2018). Such systems pose an additional challenge, with taxa inhabiting them expected to exhibit refugial distributions today (Galbreath et al. 2009, 2010; Stewart et al. 2010). Because of this, in addition to many ancestral populations likely being extinct in areas no longer suitable for the species, isolation in these systems might be too recent for a clear genetic signature to be apparent. Hence, it is possible that current population genetic patterns in these systems correspond to subtler characteristics of past and present environments, such as the degree of suitability of habitats that have remained continuously occupied by the species (i.e., affecting population sizes and associated demographic processes such as dispersal).

Among high-elevation tropical ecosystems, those of the Neotropics hold great promise for improving our understanding of the effects of past climate change on mesic montane biodiversity. In this region, substantial temperature gradients exist across elevation, with many mountains being sufficiently high to foster the formation of glaciers during past and present time periods (Hooghiemstra and Van der Hammen 2004; Lachniet 2004; Bush et al. 2009). Additionally, the region's topographic complexity provides landscapes ripe for addressing not only issues regarding range contraction and expansion per se, but also the critical effects of: 1) changing patterns of isolation and connectivity among populations; and 2) differences in levels of environmental suitability across time. In fact, the interaction between elevational zonation of taxa and past climatic oscillations has long been proposed as a hypothesis to explain the high levels of biodiversity observed today in this region—i.e., through cycles of colonization followed by isolation and divergence (Janzen 1967; Weir 2009; Cadena et al. 2012; Fjeldså et al. 2012). Although intraspecific phylogeographic approaches represent a viable way to address this hypothesis, few such studies exist; consequently, it remains unclear how past climatic changes affected species-level diversification in this region or in other tropical mountains (Navarro-Sigüenza et al. 2008; Weir et al. 2008; Streicher et al. 2009).

We employ a phylogeographic approach to assess the effects of Late Quaternary climatic oscillations in the diversification of tropical montane taxa associated with cool, mesic conditions in one such topographically complex system: the mountains of Costa Rica and western Panama. Collectively referred to as the Talamancan Province, these mountains are embedded within the biodiversity hotspot of Mesoamerican highlands that extends from Mexico through Central America (Savage 2002; Weir 2006; Gardner and Carleton 2009). Important phylogenetic breaks above the species level have been documented for a wide variety of montane taxa across "sky islands" in this hotspot, with multiple species being endemic to the Talamancan Province in particular (Hernández-Baños et al. 1995; García-Moreno et al. 2006; Cadena et al. 2007; Bonaccorso 2009).

Specifically, we integrate ecological niche models of species distributions (hereafter "niche models") with population genetic analyses to test the effects of Late Quaternary climate change on population demography and intraspecific diversification. Niche models allow characterization of climatic conditions associated with abiotic or habitat constraints on species, allowing estimates of their potential geographic distributions (Kearney 2006; Godsoe 2010; Peterson et al. 2011). By retrojecting these models into past time periods, and mapping patterns of inferred environmental suitability across the landscape, the predicted effects of past climatic oscillations can then be tested explicitly with molecular data (Knowles et al. 2007; Carnaval et al. 2009). We do so employing a comparative approach (Bermingham and Moritz 1998), focusing on two species of distantly related rodents endemic to the Talamancan Province that markedly overlap in their elevational ranges: *Reithrodontomys creper* and *Nephelomys devius*. Both species occur in montane areas throughout most of the system, yet they differ in the particular elevational bands they inhabit, *R. creper* being restricted to even higher elevations than *N. devius*. This comparison allows us to detect patterns that might be common across taxa, as well as discover any species-specific responses (Hugall et al. 2002; Stewart et al. 2010).

In contrast to most studies integrating niche models and molecular data, we incorporate a particular basic ecological principle—the expected positive relationship between environmental suitability and population abundance—and assess how phylogeographic inferences can benefit from considering it. Strong links have been established between environmental suitability, population demography, and the evolutionary structure of species ranges (Brown 1984; Brown et al. 1995; Guo et al. 2005). In general, species are expected to reach higher abundances in environments best matching their requirements; in consequence, the demographic and evolutionary fate of the species will be mostly determined by populations inhabiting such optima (Holt 1996; Gaston 2003; Kawecki 2008). This principle is already implicit in most niche models, which produce outputs reflecting different levels of suitability (Peterson et al. 2011; Soley-Guardia et al. 2014; Phillips et al. 2017). Substantial recent empirical research has addressed this topic, supporting a positive relationship between suitability and abundance (or its proxies) in most instances (Nagaraju et al. 2013; Weber et al. 2017; but see Osorio-Olvera et al. 2019 for caveats). Nevertheless, information regarding relative suitability is rarely incorporated explicitly into phylogeographic studies that make use of niche models. Instead, such research typically focuses on whether environments were suitable or not. Here, we assess the utility of incorporating the suitability–abundance principle in a simple way: discerning between two types of suitability through time. These correspond to sufficient suitability (environments suitable to the species but not highly so), and optimal suitability (environments most suitable to the species). We propose that incorporating such differences in suitability will enrich phylogeographic studies addressing environmental stability through time. This might be especially informative for taxa currently experiencing range contraction, where current genetic patterns are expected to reflect subtler differences related to the level of environmental suitability in an otherwise vastly suitable past.

To achieve these goals, we built niche models for each rodent species and retrojected them to the two climatic extremes of the most recent glacial–interglacial cycle. These models are used as the basis of the following predictions, which we then test with data from a mitochondrial and a nuclear marker gathered across the ranges of these species:

Prediction 1: Current patterns of genetic variation across space reflect potential connectivity among populations through time. Specifically, we predict that populations in areas that have remained the most isolated over all examined time periods will show the highest genetic structuring (i.e., more endemic genetic variants relative to other populations). Similarly, divergence should be highest between populations that have experienced little or no potential for connectivity through time.

Prediction 2: Genetic diversity within populations has been affected by both the degree of environmental suitability and its stability through time. Because optimal environments should tend to support larger population sizes than environments of sufficient but lower suitability, we predict that genetic diversity will be highest in areas where environmental conditions remained optimal despite climatic fluctuations (areas that we here term optimal refugia). Similarly, we predict that, outside of areas that were continuously suitable, strong changes in population size occurred only wherever the degree of suitability varied considerably through time (i.e., not in areas that consistently had the same level of suitability, either optimal or sufficient).

Prediction 3: Whereas we expect that past climatic changes caused similar effects on the studied species regarding the potential for connectivity and stability of suitable environments (i.e., both species responding in the same direction), we predict that effects on suitability and population genetics were stronger for the species restricted to higher elevations (*R. creper*), for which the passes separating mountaintops are more likely to have represented environmental barriers to dispersal and population establishment and persistence (Colwell and Rangel 2010; Cadena et al. 2012).

Materials and Methods

*Study system.—*The highlands of Costa Rica and western Panama consist of four main mountain ranges that run with a northwest–southeast orientation following the Mesoamerican fault (the Guanacaste, Tilarán, Central, and Talamanca ranges; Fig. 1). This relatively young montane system started forming ~22–5 million years ago, the oldest ranges achieving near-present heights 1 million year ago, and the youngest ones as recent as 60,000 years ago (Denyer and Kussmaul 2003; Driese et al. 2007; Vargas Ulate 2009). Currently, these highlands are characterized by evergreen cloud forests (typically occurring between 1,800 and 3,000 m), with premontane rainforests below those elevations and open-vegetation *páramo* occurring above them. The lowest mountain passes are characterized by evergreen or deciduous tropical rainforests (McCain 2004; Kapelle and Horn 2005; Fjeldså et al. 2012).

Much remains to be known regarding the geologic past of this region, but existing evidence indicates that both climate and the elevational zonation of vegetation types changed drastically over the glacial phases of the Late Quaternary (Driese et al. 2007; Bush et al. 2009). For instance, during the last glacial maximum (~21,000 years ago), temperatures have been estimated to have been 8–10°C lower, with multiple glaciers forming on the highest peaks of the Talamanca Range, including some of considerable extent (2–35 km^2—Islebe and Hooghiemstra 1997; Lachniet and Seltzer 2002; Bush et al. 2009). Pollen deposits in this region are scarce, but those studied in Talamanca suggest that the tree line was depressed as much as 1,400 m down the mountain slopes (Hooghiemstra et al. 1992; Driese et al. 2007), an estimate closely matching others from Panama and Guatemala for the same time period (Bush et al. 2009). Given the topographic landscape of the region, such vegetational displacements lead to the expectation of higher connectivity for montane taxa during glaciations (see also Ramírez-Barahona and Eguiarte 2013, 2014).

The small-mammal fauna of these mountains is characterized by a typically co-occurring assemblage of rodents and shrews largely endemic to the region (McCain 2004, 2006; Reid 2009). Among these, the rodents *R. creper* and *N. devius* represent a particularly interesting pair of species. Both are commonly encountered species with similar geographic ranges; yet, they have slight differences in habitat associations and elevational zonation. Both are endemic to three of the four mountain ranges, being apparently absent from that of Guanacaste, farthest to the west (Percequillo 2003; Carleton and Musser 2005; Reid 2009). *Reithrodontomys creper* typically occurs at 1,800–3,400 m, where it inhabits cloud forests and occasionally open *páramo*; *N. devius* occurs at lower elevations (typically 1,400–2,000 m), inhabiting cloud forests and premontane wet forests but not open *páramo* (McCain 2004, 2006; Reid 2009). These species belong to two different subfamilies of the Muroidea that diverged 15–19 million years ago and which diversified on different landmasses before the closure of the Panamanian Isthmus (Steppan et al. 2004; Carleton and Musser 2005); as such, they provide independent evidence regarding possible common processes occurring in the region.

*Ecological niche models.—*Ecological niche models (often also called species distribution models) are correlative approaches used to estimate species potential geographic distributions based on inferences regarding their Grinnellian niches obtained from occurrence data and GIS-based environmental predictor variables (Kozak et al. 2008; Peterson et al. 2011). Following modeling practices chosen to meet critical assumptions for the data at hand (Anderson 2012, 2013), these methods can provide estimates of the areas that are abiotically suitable for a species and where it can occur given appropriate biotic contexts and sufficient dispersal capacities (Araújo and Guisan 2006; Peterson et al. 2011).

For each species, we modeled the suitable area using current data, and then retrojected that model to two past climatic extremes of the Late Quaternary: the last glacial maximum (~21,000 years ago; coldest) and the mid-Holocene (~6,000 years ago; warmest). These two time periods are considered to reflect opposite environmental extremes during the last glacial–interglacial transition (Lomolino et al. 2006); we assume that intermediate environmental conditions led to patterns of suitability lying between these extremes. The estimates of abiotic suitability at these time periods were then used to calculate indices of potential connectivity and stability through time, yielding the predictions that we tested with genetic data.

We obtained occurrence data from multiple sources, verifying the taxonomic identification of every record by examining museum specimens georeferencing them via consultation

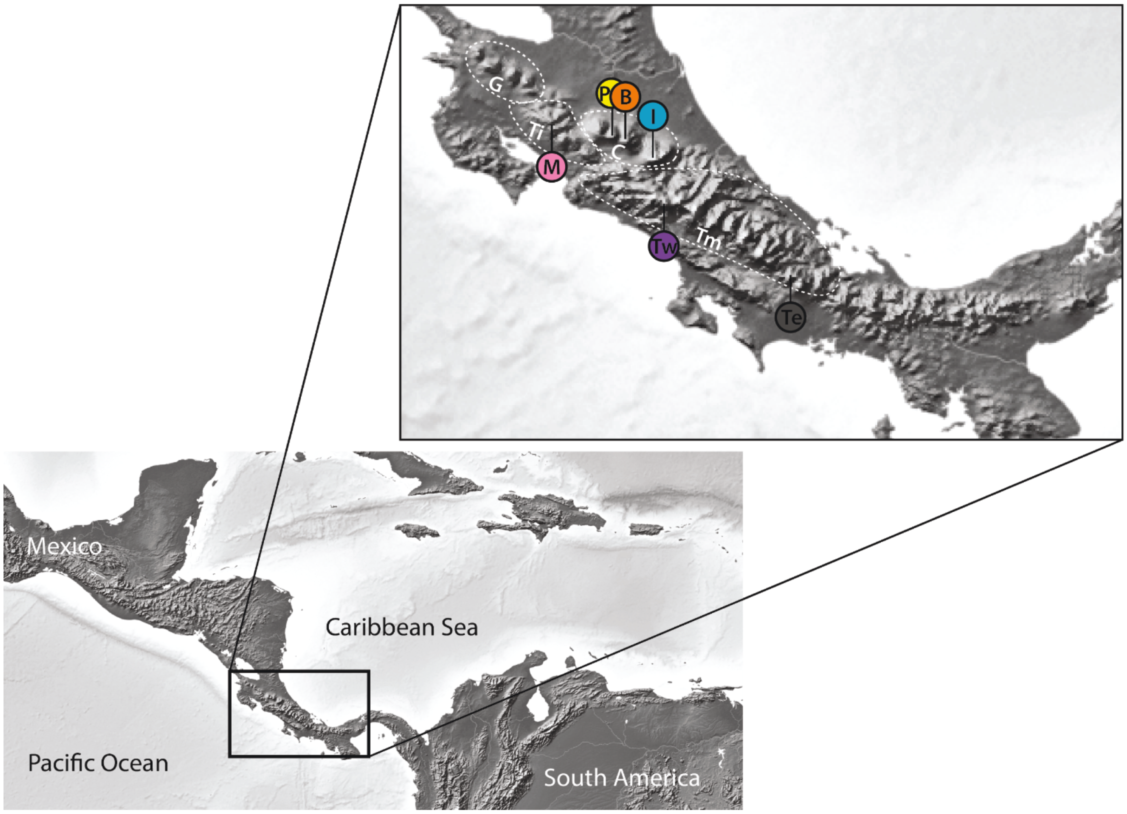


Fig. 1.—Elevation map of Central America, with study system enlarged in the inset. The four main mountain ranges of Costa Rica and western Panama are indicated with dashed ellipses and labeled G: Guanacaste, Ti: Tilarán, C: Central, and Tm: Talamanca. Pins denote sites for which we obtained tissue samples for molecular analyses (from several nearby localities), spanning the three ranges inhabited by the focal taxa. The color scheme used to denote each site in the electronic version is maintained throughout the other figures. From west to east, M: Monteverde, P: Poás, B: Barva, I: Irazú, Tw: Talamanca west, and Te: Talamanca east. Map retrieved from NATURAL EARTH (naturalearthdata.com).

of field notes, maps, gazetteers, and other sources (Lozier et al. 2009; Newbold 2010; Appendix I; details in Supplementary Data SD1). To reduce the likelihood of artifactual inferences stemming from the sampling biases typically present in occurrence data sets (i.e., certain areas more heavily sampled; Hortal et al. 2008), we employed a novel approach that builds on existing techniques for spatial filtering (Boria et al. 2014). This consisted of building preliminary niche models to estimate the optimal distance at which data sets should be spatially filtered without losing valuable environmental information (i.e., "tuning" for the optimal filtering distance; Supplementary Data SD1). For both species, the best-performing data set corresponded to the complete set of unique records (i.e., without spatial thinning: *R. creper*, $n = 48$; *N. devius*, $n = 57$; available in Supplementary Data SD2).

For the climatic data, we used the complete set of the 19 WorldClim bioclimatic variables (version 1.0—Hijmans et al. 2005), which describe temperature and precipitation patterns likely relevant to the focal species and have proven successful for modeling many taxa, including Neotropical rodents (Waltari et al. 2007; Anderson and Raza 2010; Soley-Guardia et al. 2016). We obtained estimates of these variables for the mid-Holocene and last glacial maximum from the Community Climate System Model (CCSM3—Collins et al. 2006). Even though additional paleoclimatic reconstructions are available, we chose CCSM because it has yielded paleodistributions more congruent with phylogeographic data in other studies (Fernández-Mazuecos and Vargas 2013; Ramírez-Barahona and Eguiarte 2014). We limited the modeling extent to areas that are likely to have been available for dispersal by the species, reducing biases in suitability inferences stemming from factors unrelated to the environmental predictors themselves (Anderson and Raza 2010; Barve et al. 2011; Supplementary Data SD1).

We calibrated the models using MaxEnt v. 3.3.3k (Phillips et al. 2006), optimizing parameterization by extensive "tuning" trials under a spatially defined *k*-fold cross-validation approach (i.e., segregating data into subsets iteratively used for calibration and evaluation; available in Supplementary Data SD2). We did this using the R package ENMeval (Muscarella et al. 2014; R Core Team 2014). This approach selects the MaxEnt settings that resulted in the models with the best average predictive performance (which we gauged as low omission of evaluation records, and high ability to discriminate suitability from the background environment; Supplementary Data SD1). By doing so, we aimed to optimize dimensionality (number of environmental variables incorporated into the model) and complexity (numbers and types of parameters describing the species' response to those variables) while minimizing overfitting to the specific data set (Radosavljevic and Anderson 2014; Soley-Guardia et al. 2014).

Employing the settings deemed optimal via the tuning procedure in ENMEVAL, we built MAXENT models for the present time period using the spatially segregated subsets of occurrence data (available in Supplementary Data SD2). Since we also retrojected each of these models onto the past, this led to a suite of models for each time period, each built with a different subset of the total occurrence records. This procedure allowed us to estimate uncertainty in the predictions of suitability, as well as to assess model robustness to extrapolation into novel environments when retrojecting (Wenger and Olden 2012; Muscarella et al. 2014; Supplementary Data SD1). We chose MAXENT's default option of clamping suitability response curves when extrapolation into novel environments was necessary (Elith et al. 2010). Overall, these models showed high performance when predicting independent data sets and proved robust to differences in the calibration data sets and alternative extrapolation methods (Supplementary Data SD1). For this reason, we used these models to generate ensemble MAXENT predictions for each time period; we did so simply by averaging the logistic prediction values obtained in each of the models built with the spatially segregated subsets of the data. These ensemble predictions were used for all subsequent analyses, where they were transformed into spatially explicit quantifications of potential for connectivity and environmental stability through time (see below). In so doing, we assume that: 1) the species' niches have remained stable across the time periods analyzed (i.e., conserved niches—Wiens et al. 2010); and 2) at the spatial scale employed, biotic aspects important in determining the species' distributions are consistently correlated with, or superseded by, the abiotic bioclimatic variables used (Anderson 2013; Lira-Noriega et al. 2013; Saupe et al. 2013).

Testable predictions from niche models.—To generate predictions of potential connectivity across the landscape, for each species we transformed the ensemble MAXENT prediction to both discrete and continuous formats. For the discrete format, we converted the logistic values of the ensemble prediction (ranging from 0 to 1) into three categories of suitability that correspond to inferences regarding population demography: 1) unsuitable—where populations cannot persist, 2) sufficiently suitable—where environmental conditions are adequate for population growth and persistence, and 3) optimally suitable—where environmental conditions are best for population growth and persistence. These categories were created according to thresholds obtained from the occurrence data and the suitability values they received in the ensemble prediction for the present time period; the respective thresholding values were then applied to the ensemble predictions of past suitability to yield the same categories. Specifically, we defined as unsuitable those areas exhibiting suitability values below that assigned to the least-suitable occurrence record (i.e., corresponding to MAXENT's minimum training presence threshold averaged across the models yielding the ensemble prediction). Sufficient suitability was assigned to areas receiving suitability values at least as high as this least-suitable occurrence record, but lower than the median suitability assigned to occurrence records. Optimal suitability was assigned to all areas with values at or above the median suitability associated with occurrence records (Supplementary Data SD1). For the continuous format, for each time period, we created a layer denoting the environmental cost of connectivity across the landscape; this consisted of a simple inversion of suitability values (i.e., subtracting them from 1). In this way, the grid cells with the lowest suitability exhibited the highest cost of connectivity. To calculate the specific cost of connectivity between two sites, we summed all values found along the least-cost path (Chan et al. 2011; Brown 2014; Supplementary Data SD1).

To generate predictions regarding temporal patterns of suitability, we then employed a simple yet novel approach that considers changes in the categorical levels of suitability inferred above. For this analysis, we only considered changes occurring between the last glacial maximum and the mid-Holocene. Taken together, these periods encompass a range of environmental conditions that include current ones; consequently, any change in suitability over the glacial–interglacial transition should be most prominent between these two periods. To show these changes in degree of suitability over time, we overlapped the discrete suitability maps of the last glacial maximum and mid-Holocene and classified areas into four types according to how their level of suitability varied between those time periods. The types are: areas that were and remained sufficiently suitable over time (sufficient refugia), areas that were and remained optimally suitable over time (optimal refugia), areas where suitability increased categorically during the transition to the mid-Holocene (suitability increase), and those where suitability decreased categorically during that transition (suitability decrease). The remaining areas correspond to those that have been unsuitable since the last glacial maximum or became so by the mid-Holocene, where to our knowledge the species is absent, or at least not documented by rodent-sampling efforts in the region.

Molecular data.—Through field work and loans from natural history museum collections, we obtained tissue samples from multiple localities corresponding to six general sites that span the three mountain ranges occupied by both species (Fig. 1; *R. creper*, $n = 58$ individuals; *N. devius*, $n = 51$; Supplementary Data SD1). Most tissues were collected between 2010 and 2012; those corresponding to the site of Monteverde were collected between 1987 and 1989, or between 2000 and 2002. All these sites are located in vast swaths of forests that are remote or under highly effective governmental protection; hence, we assume that changes in population size due to local anthropogenic causes are unlikely. Collection of all specimens for this study followed guidelines from the City College of New York Institutional Animal Care and Use Committee (IACUC), as well as the American Society of Mammalogists (Gannon and Sikes 2007; Sikes et al. 2011; for most recent guidelines see, Sikes et al. 2016), under permit numbers 119-2010 and 109-2011-SINAC of the Ministerio de Ambiente y Energía de Costa Rica (MINAE).

We extracted DNA from liver, heart, or muscle tissue using a salt-precipitation protocol (Miller et al. 1988) and subsequently amplified and sequenced two molecular markers that should provide inferences at different time scales (Avise 2000; Brito and Edwards 2009; details in Supplementary Data SD1). Specifically, we obtained sequences for the mitochondrial cytochrome *b* gene (*Cytb*—Smith and Patton 1993), and for the nuclear ACOX2 intron 3 (*ACOX2-3*), which flanks a single-copy gene in mammals (the acyl-coenzyme A oxidase 2, peroxisomal—Igea et al. 2010; for GenBank accession numbers, see Supplementary Data SD3). Regarding the *Cytb* gene, for *R. creper* we were able to amplify a fragment of 814 bp; for *N. devius* we amplified the entire gene, consisting of 1,149 bp (except for one sample for which sequencing was unsuccessful; hence, $n = 50$ for this marker in this species). For the nuclear *ACOX2-3* marker, amplified fragments consisted of 432 bp in *R. creper* and 496 bp in *N. devius* (primers and protocols for both markers are detailed in the Supplementary Data SD1). We used PHASE 2.1.1 (Stephens et al. 2001) to obtain the most probable haplotypes presented by each diploid individual for the nuclear marker (all inferred with probabilities > 0.93; Supplementary Data SD1).

Testing predictions.—To test Prediction 1—patterns of genetic variation across space reflect potential connectivity among populations through time—we assessed genetic structure at sampled sites and estimated the genetic divergence among them. These metrics were then interpreted against the spatial predictions derived from the niche models under the discrete and continuous approaches described above. To test predictions of connectivity stemming from the discrete approach, first we built maximum parsimony haplotype networks for each marker in R, using the packages: PEGAS, PLYR, and RESHAPE (Wickham 2007, 2011; Paradis 2010; R Core Team 2014). We expect haplotypes to be most likely shared between sites that show potential for connectivity throughout the three time periods analyzed. Second, we calculated two population genetic statistics for each pairwise comparison between sites. The first corresponds to the fixation index (F_{ST}), which can be interpreted as a relative index of population divergence due to genetic structure (Nielsen and Slatkin 2013); we calculated this in DNASP v.5.10.01 (Librado and Rozas 2009). The second corresponds to the uncorrected pairwise genetic distance (uncorrected *p*-distance), which measures the genetic divergence observed, on average, between individuals of two different populations (calculated in MEGA v. 5.05—Tamura et al. 2011). We expect that values of both these metrics will be higher for pairs of sites that have exhibited less potential for connectivity through time.

To test whether molecular data supported predictions of connectivity derived from the continuous approach, we analyzed if there was a correlation between the divergence (F_{ST} values) and environmental cost of connectivity exhibited between sites (see "Testable predictions from niche models" above) at each past climatic extreme. For this, we built matrices of F_{ST} and environmental cost-of-connectivity values, incorporating all pairwise comparisons among the six sites for which we obtained molecular data. However, environmental cost-of-connectivity values may be spatially autocorrelated (Legendre and Fortin 2010), in which case any correlation between these values and divergence may simply derive from isolation by distance (Slatkin 1993; Jenkins et al. 2010). To rule out this possibility, we incorporated a third matrix into the analysis, Euclidean distances between sites. We analyzed these three matrices together using partial Mantel tests (Smouse et al. 1986), assessing whether divergence is significantly correlated with environmental cost of connectivity, once Euclidean distances are taken into account (but see potential caveats of these analyses in Raufaste and Rousset 2001; Legendre and Fortin 2010). We performed these tests using the VEGAN package in R (Oksanen et al. 2010). Specifically, we permuted the F_{ST} values using a simple randomization procedure and allowing for the maximum number of nonduplicate effective permutations possible, while keeping constant any correlation structure between environmental cost of connectivity and Euclidean distances (Legendre and Fortin 2010). Given the low level of divergence exhibited by the nuclear marker (see "Results"), we performed these analyses for the mitochondrial marker only.

To test Prediction 2—genetic diversity within populations has been affected by both the degree of environmental suitability and its stability through time—we calculated four genetic metrics related to population sizes and their stability through time. The first two metrics correspond to haplotype and nucleotide diversity, both calculated using DNASP v.5.10 (Librado and Rozas 2009) and interpreted jointly. Haplotype diversity ranges from 0 to 1, and it decreases as populations become small, due to stronger genetic drift. Hence, it is expected to be higher in populations that have either remained constantly large or expanded (Avise 2000; Nielsen and Slatkin 2013). Nucleotide diversity is expressed as an average percentage of the difference between haplotypes (Nei 1987). It is expected to be small for populations that have had consistently low population size, decreased in size, or recently expanded (in the first two instances due to genetic drift, and in the latter due to the limited amount of time for the new haplotypes to diverge substantially from their ancestral ones—Slatkin and Hudson 1991). Taken together, we expect that both haplotype and nucleotide diversity should be low for populations in sufficient refugia and areas of suitability decrease, where presumably population sizes have been constantly small or were reduced during the current interglacial. Conversely, since we suggest that populations occurring in optimal refugia presumably attained and retained large sizes, we expect both their haplotype and nucleotide diversity to be high (Gugger et al. 2013; Oliveira et al. 2018). Lastly, since we posit that populations occurring at areas of suitability increase presumably experienced population expansion, we expect these to have a high haplotype diversity but low nucleotide diversity (Milá et al. 2000; Nuñez et al. 2011).

In addition to these two descriptive metrics, we also calculated two test statistics that differ in their power to detect changes in population size: Tajima's *D* (Tajima 1989) and Fu's *F* (Fu 1997). Note, however, that neither of these statistics can distinguish between changes in population size and natural selection, given that genetic signatures of these processes are virtually the same for a given marker (Holsinger et al. 2012). Negative significant values of Tajima's *D* and Fu's *F* are associated with population expansion, and positive significant ones with population contraction; nonsignificant values are congruent with a null hypothesis of constant population size (Tajima 1989; Fu 1997). We expect that values of these statistics should match the demographic predictions stemming from the degree of suitability and its stability through time (i.e., constant population sizes at sufficient and optimal refugia; population contraction in areas exhibiting suitability decrease; and population expansion in areas exhibiting suitability increase). Given the low level of divergence exhibited by the nuclear marker (see "Results"), we calculated these two statistics for the mitochondrial marker only. We did so in DnaSP v.5.10.01 (Librado and Rozas 2009), using the total number of mutations, not allowing for recombination, and keeping all other settings as default. We assessed their level of significance by performing 10,000 coalescent simulations based on estimated theta values.

These four genetic metrics require an explicit geographic delimitation of populations, which is typically estimated rather than known (Nielsen and Slatkin 2013). To do this, we used a simple criterion, pooling together geographic sites with the lowest F_{ST} values (preliminary analyses with the STRUCTURE software were inconclusive and did not yield geographically defined populations; Supplementary Data SD1). To avoid biases stemming from this specific procedure used to define populations, we also carried out the same analyses without pooling sites (i.e., considering each of the six geographic sites as separate populations). The findings for these unpooled data were very similar; we provide them in the Supplementary Data SD1 and mention notable trends in the "Results." Finally, because of potentially high georeferencing errors in one sample of *R. creper* from Panama (see Appendix I), we removed it from all these analyses, which require fine spatial delimitation (hence, $n = 57$).

RESULTS

In general, the niche-model outputs matched expectations for both species regarding patterns of potential connectivity and degree of suitability during current and past time periods (Figs. 2 and 3). These outputs suggest that, over the transition from the last glacial maximum, through the mid-Holocene, to the present, suitable environments have constantly existed along the mountain ranges. Some of these ranges have had constant potential for connectivity, and others only did during the glacial maximum; however, such connectivity never occurred through areas of optimal suitability. Instead, optimally suitable environments have been exclusively restricted to the highest parts of the ranges throughout the time periods analyzed, occurring as patches that have remained constantly isolated from one another.

As expected, the specifics of this overall pattern varied between the two rodent species. The species typically inhabiting higher elevations (*R. creper*) showed a less extensive suitable area throughout the periods analyzed. It exhibited less potential for connectivity under both categories of suitability during all time periods, but especially so during the mid-Holocene. Notably, whereas the extent and distribution of sufficiently suitable environments varied little across time, optimally suitable environments showed low stability (Figs. 2 and 4A). In contrast, the species inhabiting lower elevations (*N. devius*) showed a more extensive suitable area overall, exhibiting more potential for connectivity during all time periods. Additionally, for *N. devius*, the extent and distribution of all suitable environments varied little across time (i.e., showing high stability; Figs. 3 and 4B).

In general, these spatial predictions of connectivity and stability were supported by the genetic analyses in both species, but especially so in the one inhabiting higher elevations, *R. creper*. For both species, the mitochondrial marker showed substantially more variation than the nuclear one. Therefore, we focus mostly on this marker but mention noteworthy patterns for the nuclear marker where relevant (detailed results can be found in Supplementary Data SD1, including the descriptive statistics for each marker).

Reithrodontomys creper.—For this species, environments with sufficient suitability have constantly occurred along the slopes of all ranges, at some periods extending into the mountaintops; in contrast, optimally suitable environments have remained restricted to specific mountaintops, sometimes disappearing during a particular time period (Fig. 2). Notably, environments of optimal suitability have been absent from the Tilarán Range, as well as from the Guanacaste Range, which the species does not inhabit. The sufficient suitability level yielded predictions of constant connectivity among the three distinct inhabited mountain ranges and their constituent peaks, the sole exception being the Tilarán Range, which appeared isolated during all time periods. Conversely, at the optimal suitability level, all mountain ranges appeared isolated from one another throughout all time periods, as were their constituent peaks. Unexpectedly, this was also true for the seemingly contiguous, and continuously high, Talamanca Range. There, optimally suitable environments occurred in large disjunct areas, and even sufficiently suitable environments were dissected by a narrow gap in the middle throughout all time periods.

Regarding Prediction 1—patterns of genetic variation across space reflect potential connectivity among populations through time—under the discrete approach, data from the mitochondrial marker best supported inferences stemming from the category of optimal suitability, which predicted constant isolation of sampled sites. This marker showed substantial structure not only across the three ranges, but also among sites within the same range (Fig. 2). There was only one haplotype shared between sites, the Poás and Irazú volcanoes of the Central Range. F_{ST} values were high for comparisons involving sites from different ranges, yet substantially lower for comparisons between sites of the same range (Table 1). In particular, F_{ST} values were highest for every comparison involving the site from the Tilarán Range, predicted as isolated according to both optimal and sufficient suitability levels. Similarly, uncorrected *p*-distance values were higher between sites belonging to different ranges, and again, particularly so in comparisons involving the Tilarán Range site (1.2–1.4%; Table 1). The lowest uncorrected *p*-distance value was found between the western and eastern

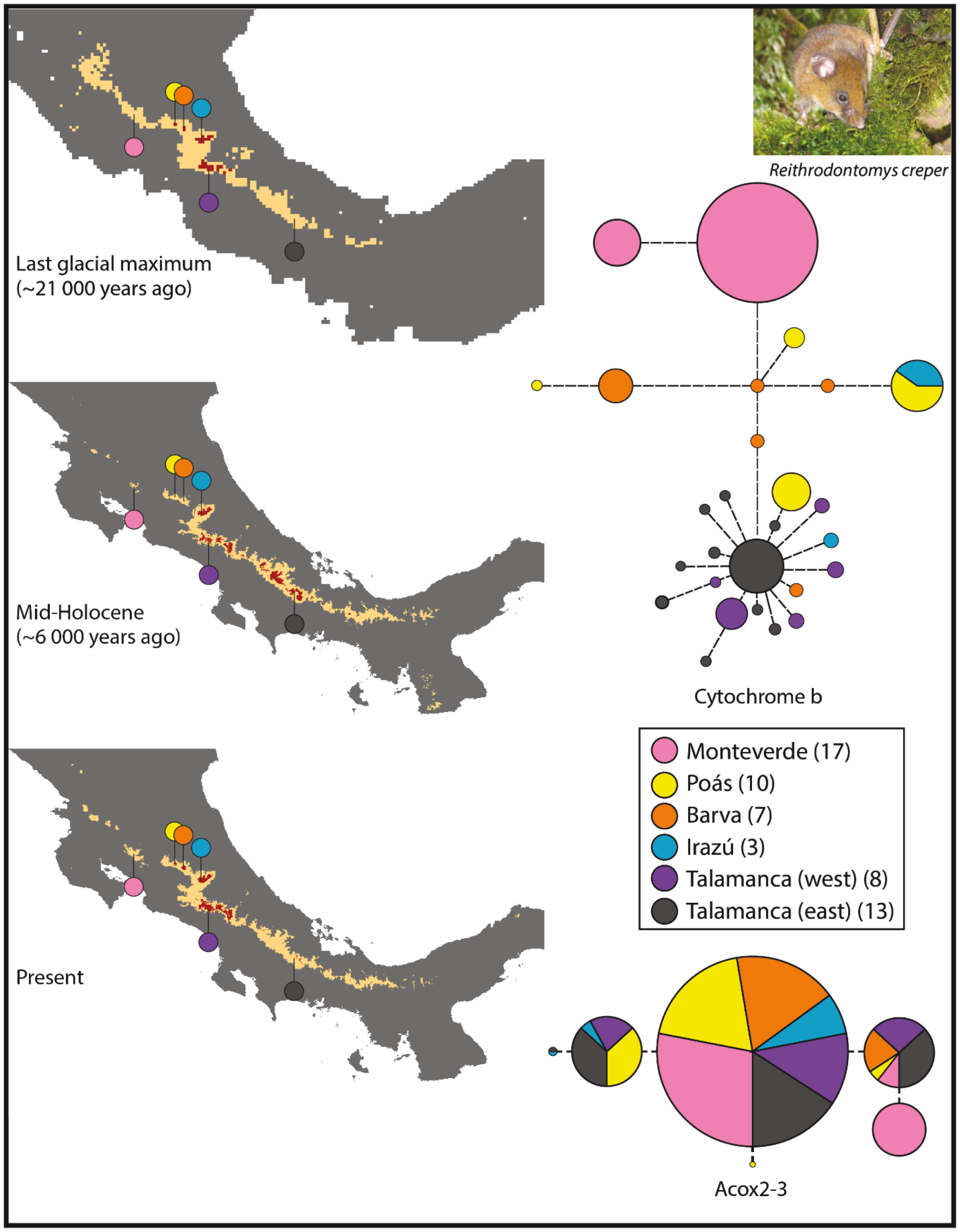


Fig. 2.—Environmental suitability and genetic structure of *Reithrodontomys creper* in Costa Rica and western Panama. Maps derived from niche models denote the potential for connectivity at three time periods. Map colors designate three different categories of suitability; gray: unsuitable areas (with values below the lowest presence threshold of 0.053); light orange: sufficiently suitable areas (values between the lowest presence and median suitability thresholds); maroon: optimally suitable areas (with values equal or above the median suitability threshold of 0.628). Haplotype networks are given for the mitochondrial and nuclear markers; gaps in connecting lines indicate inferred number of mutation steps between haplotypes. Each circle represents a unique haplotype, with size being proportionate to frequency. The colors of each circle indicate the sampling sites where that particular haplotype was found. Sampling sites are marked with colored circles in the suitability maps and detailed in the inset box (the number of samples per site is given in parenthesis). Note: circle sizes only proportional within genetic markers; one sample from Talamanca (east) may actually correspond to a locality further to the east (see Appendix I).

ends of Talamanca (0.41%; Table 1). Tellingly, *p*-distances were similar between sites that were close in geography but that showed little potential for connectivity and sites separated by twice the geographic distance but showing higher potential for connectivity (Fig. 5A). The first prediction was also supported following the continuous approach, but only for estimates of connectivity during the mid-Holocene. Specifically, the partial Mantel test showed a high significant correlation between F_{ST} values and environmental cost of connectivity during that time period ($r = 0.9$, $P = 0.011$), but not so during the glacial maximum ($r = 0.7$, $P = 0.115$).

Overall, the nuclear marker showed much less divergence (average uncorrected *p*-distance = 0.24%, versus 0.88% for *Cytb*) and barely any geographic structuring, with most of the few haplotypes being shared across ranges (Fig. 2; see also Supplementary Data SD1). As such, divergence between

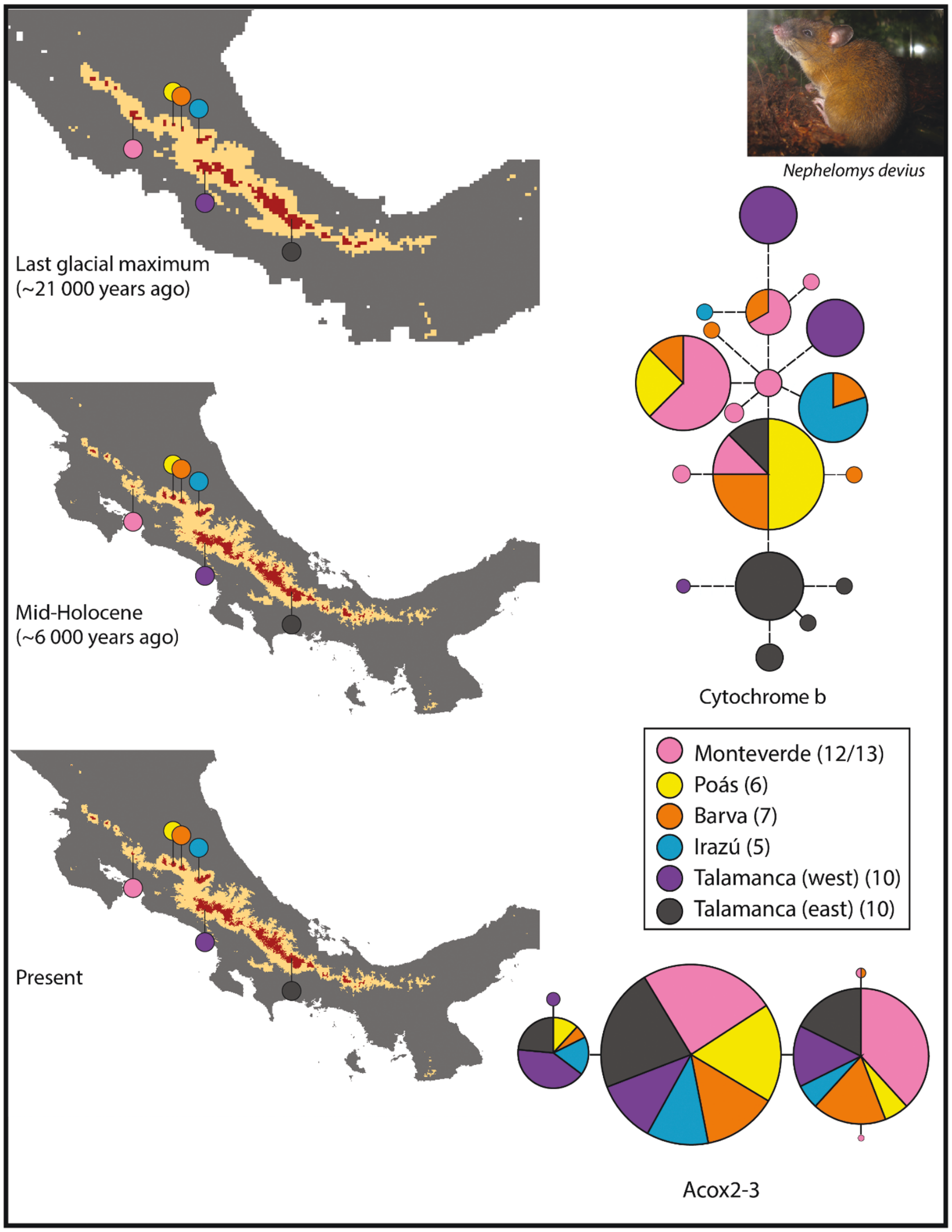
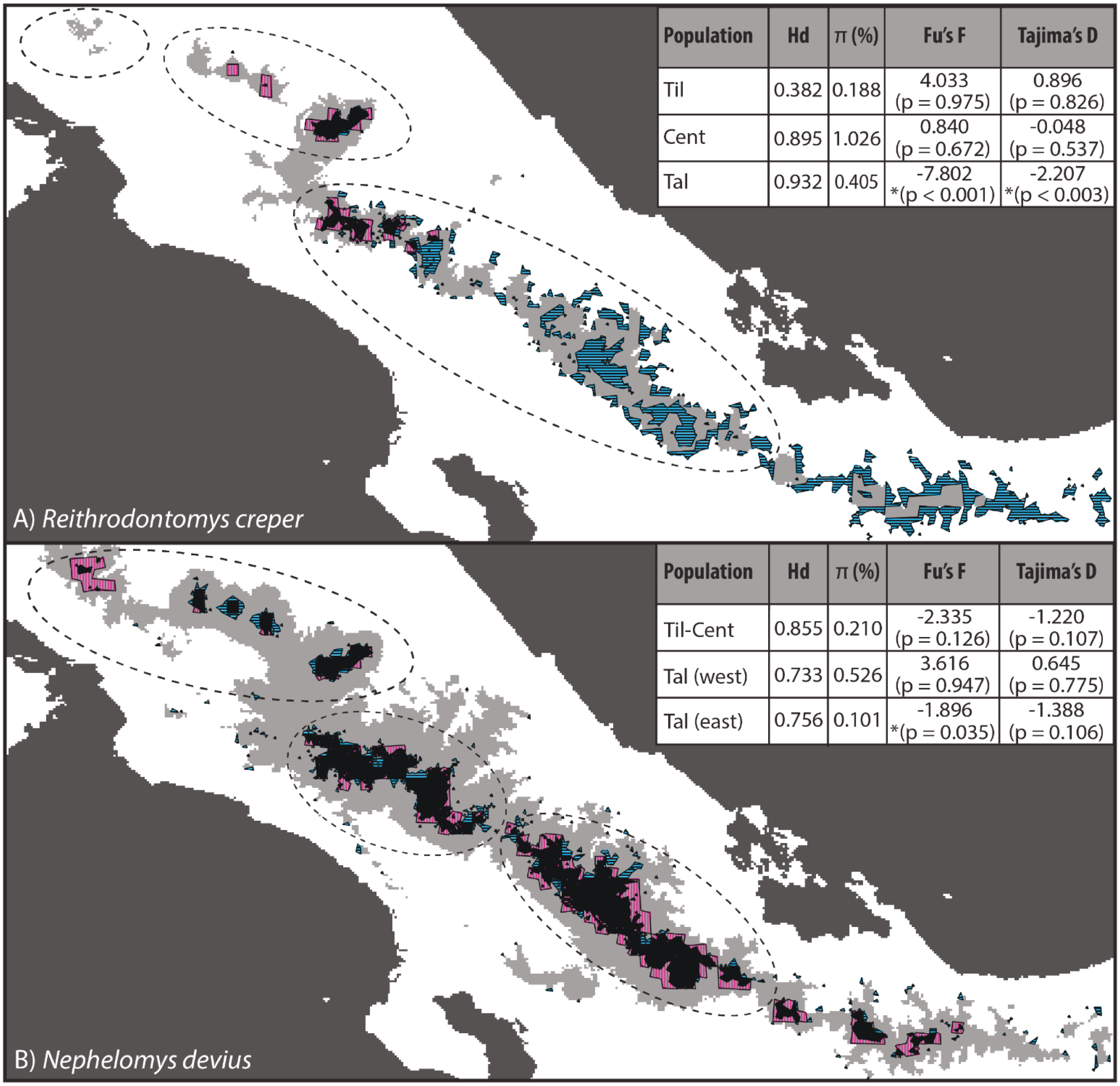


Fig. 3.—Environmental suitability and genetic structure of *Nephelomys devius* in Costa Rica and western Panama. Maps derived from niche models denote the potential for connectivity at three time periods. Map colors designate three different categories of suitability; gray: unsuitable areas (with values below the lowest presence threshold of 0.212); light orange: sufficiently suitable areas (values between the lowest presence and median suitability thresholds); maroon: optimally suitable areas (with values equal or above the median suitability threshold of 0.619). Haplotype networks are given for the mitochondrial and nuclear markers; gaps in connecting lines indicate inferred number of mutation steps between haplotypes. Each circle represents a unique haplotype, with size being proportionate to frequency. The colors of each circle indicate the sampling sites where that particular haplotype was found. Sampling sites are marked with colored circles in the suitability maps and detailed in the inset box (the number of samples per site is given in parenthesis; for Monteverde, the dash separates the sample size for each marker, given unsuccessful sequencing of one sample for the cytochrome *b* gene). Note: circle sizes only proportional within genetic markers.

sites was generally low (maximum values of 0.39 and 0.35% for F_{ST} and uncorrected *p*-distances, respectively) and did not follow any clear pattern (e.g., both F_{ST} and *p*-distance values were commonly higher for pairwise comparisons within ranges than for ones among them). However, one result was consistent with the divergence observed in the mitochondrial marker: the highest F_{ST} (0.24–0.39) and *p*-distance values (0.23–0.35%) were unambiguously restricted to all comparisons involving the Tilarán Range (Supplementary Data SD1), the site showing the most environmental isolation, and also harboring the only abundant haplotype endemic to a region (Fig. 2).

Prediction 2—genetic diversity within populations has been affected by both the degree of environmental suitability and its stability through time—was highly supported by data from the mitochondrial marker (Fig. 4A). Overall, there was a striking congruence between expected and inferred population



Population	Hd	π (%)	Fu's F	Tajima's D
Til	0.382	0.188	4.033 (p = 0.975)	0.896 (p = 0.826)
Cent	0.895	1.026	0.840 (p = 0.672)	-0.048 (p = 0.537)
Tal	0.932	0.405	-7.802 *(p < 0.001)	-2.207 *(p < 0.003)

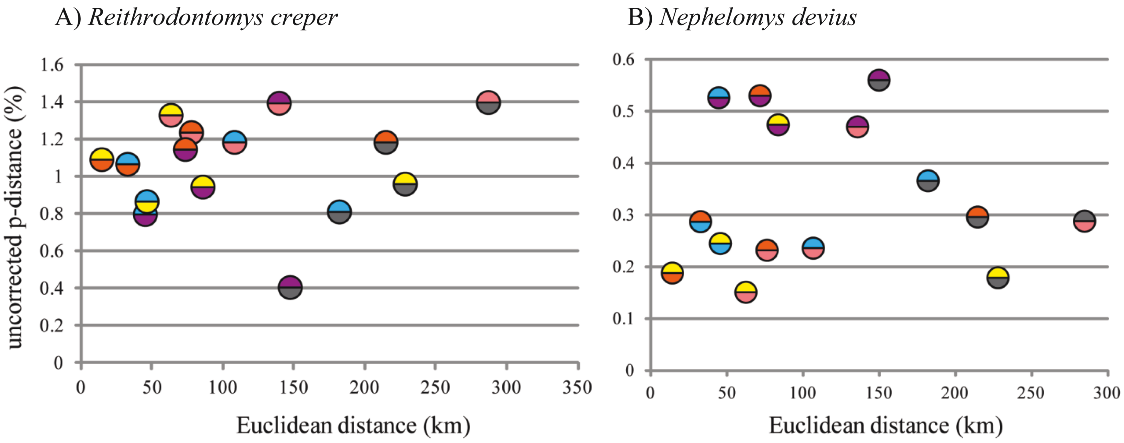
Population	Hd	π (%)	Fu's F	Tajima's D
Til-Cent	0.855	0.210	-2.335 (p = 0.126)	-1.220 (p = 0.107)
Tal (west)	0.733	0.526	3.616 (p = 0.947)	0.645 (p = 0.775)
Tal (east)	0.756	0.101	-1.896 *(p = 0.035)	-1.388 (p = 0.106)

Fig. 4.—Comparisons of environmental stability for each focal species in Costa Rica and western Panama between the last glacial maximum and the mid-Holocene, and genetic metrics used to assess changes in population sizes. A) *Reithrodontomys creper*; B) *Nephelomys devius*. White: unsuitable areas, where environments remained unsuitable (or became so at the mid-Holocene); gray: sufficient refugia, where environments remained suitable but not highly so (ranging between the lowest presence and median suitability thresholds); black: optimal refugia, where environments remained highly suitable (above the median suitability threshold); cyan horizontal hatches: suitability increase, denoting areas that increased in categorical suitability in the transition to the mid-Holocene (mostly from sufficiently to optimally suitable; transitions from unsuitable to sufficiently suitable can be seen in the borders of sufficient refugia, toward the lowlands); magenta vertical hatches: suitability decrease, denoting areas where suitability decreased from optimal to sufficient in the transition to the mid-Holocene. Genetic metrics were calculated for the pooled populations demarcated with the dashed circles using the cytochrome *b* data; * denotes statistical significance. Hd: haplotype diversity; π: nucleotide diversity; Til: Tilarán; Cent: Central; Tal: Talamanca.

demography at sufficient and optimal refugia, as well as at sites of suitability increase. Specifically, three main populations were delimited for this species, each one corresponding to a particular mountain range. According to the overlapped predictions of suitability across time, the only mountain range considered exclusively as a sufficient refugium was that of Tilarán. As expected, this population showed the lowest haplotype and nucleotide diversity (0.382 and 0.188%, respectively),

Table 1.—F_{ST} values (above matrix diagonal) and uncorrected *p*-distances (below matrix diagonal, in italics) between sampled sites for the cytochrome *b* marker of *Reithrodontomys creper* in Costa Rica and western Panama. Sites are ordered in a west–east orientation. Uncorrected *p*-distances are given in percentages; average *p*-distance across all sampled individuals was 0.878%.

R. creper	Monteverde	Poás	Barva	Irazú	Talamanca (west)	Talamanca (east)
Monteverde	—	0.533	0.528	0.608	0.787	0.787
Poás	*1.333*	—	0.064	−0.038	0.233	0.239
Barva	*1.240*	*1.091*	—	0.192	0.402	0.414
Irazú	*1.182*	*0.865*	*1.066*	—	0.295	0.296
Talamanca (west)	*1.392*	*0.953*	*1.160*	*0.810*	—	−0.001
Talamanca (east)	*1.397*	*0.961*	*1.186*	*0.813*	*0.405*	—


A) *Reithrodontomys creper*

B) *Nephelomys devius*

Fig. 5.—Relationship between genetic and geographic distances for A) *Reithrodontomys creper* and B) *Nephelomys devius* in Costa Rica and western Panama. Each plot shows uncorrected *p*-distances of the cytochrome *b* marker between pairs of sampled sites as a function of geographic (Euclidean) distances. The two sites being compared are indicated by numbers in the boxes (or colors inside the circles of the electronic version, matching the scheme of the rest of the figures); they follow a west-to-east ordering: 1: Monteverde, 2: Poás, 3: Barva, 4: Irazú, 5: Talamanca west, and 6: Talamanca east. Note: different scales used for each species.

and the genetic statistics did not reject a constant population size ($P > 0.826$; Fig. 4A). The other two mountain ranges presented a mosaic of optimal refugia and areas that changed in suitability, although one or the other dominated the landscape. In the Central Range, optimal refugia prevailed across mountain peaks, although a notable suitability decrease occurred in western peaks. Matching expectations for an optimal refugium, the Central population exhibited high haplotype and nucleotide diversity (0.895 and 1.026%, respectively), and the genetic statistics did not reject a constant population size ($P > 0.537$; Fig. 4A). In Talamanca, areas showing a suitability increase prevailed. Matching expectations for such areas, the Talamanca population showed high haplotype diversity but low nucleotide diversity (0.932 and 0.405%, respectively), and both genetic statistics assessing changes in population size were statistically significant for population expansion ($P < 0.003$; Fig. 4A). In general, these molecular results still held when each geographic sampled site (i.e., mountain peak) was considered as a separate population (Supplementary Data SD1).

Nephelomys devius.—For this species, environments with sufficient and optimal suitability were constantly present in all mountain ranges throughout the time periods analyzed, the former always restricted to the slopes and the latter to the mountaintops (Fig. 3). As in *R. creper*, the sufficient suitability level yielded predictions of constant connectivity among all mountain ranges, but the optimal suitability level predicted isolation among ranges and their constituent peaks throughout all time periods. For *N. devius*, the gap between the western and eastern portions of the Talamanca Range was only apparent at the optimal level of suitability.

Regarding Prediction 1—patterns of genetic variation across space reflect potential connectivity among populations through time—under the discrete approach, data from the mitochondrial marker best supported inferences stemming from the category of sufficient suitability (contrary to *R. creper*), which predicted constant connectivity among sites. This marker showed little geographic structure, haplotypes being shared among sites and even among ranges, some being present at opposite extremes of the species' geographic distribution (Fig. 3). Notably, however, haplotypes were not shared between western and eastern ends of Talamanca, nor between those sites and the rest, with one exception. These latter results matched estimates of connectivity inferred only at the optimal suitability level. Following a similar pattern, F_{ST} values were overall much lower for this species (Table 2), although they were moderate to high in all comparisons involving either the western or eastern Talamanca sites (0.23–0.58). Uncorrected *p*-distance values were also typically higher for pairwise comparisons involving either of these Talamanca sites (0.18–0.56%; Table 2). Contrary to *R. creper*, *p*-distance values for *N. devius* were usually higher between sites farther in geography, with the exception of the aforementioned Talamanca sites (Fig. 5B). This first prediction was not

Table 2.—F_{ST} values (above matrix diagonal) and uncorrected *p*-distances (below matrix diagonal, in italics) between sampled sites for the cytochrome *b* marker of *Nephelomys devius* in Costa Rica and western Panama. Sites are ordered in a west–east orientation. Uncorrected *p*-distances are given in percentages; average *p*-distance across all sampled individuals was 0.342%.

N. devius	Monteverde	Poás	Barva	Irazú	Talamanca (west)	Talamanca (east)
Monteverde	—	0.128	−0.011	0.193	0.259	0.527
Poás	*0.152*	—	−0.026	0.381	0.350	0.462
Barva	*0.233*	*0.191*	—	0.121	0.229	0.326
Irazú	*0.237*	*0.244*	*0.289*	—	0.306	0.577
Talamanca (west)	*0.472*	*0.476*	*0.535*	*0.530*	—	0.441
Talamanca (east)	*0.289*	*0.180*	*0.296*	*0.366*	*0.561*	—

supported when following the continuous approach, however. Partial Mantel tests for this species did not show a significant correlation between F_{ST} values and environmental cost of connectivity during the last glacial maximum ($r = -0.4$, $P = 0.788$), or during the mid-Holocene ($r = -0.4$, $P = 0.800$).

The nuclear marker showed even less divergence (average uncorrected *p*-distance = 0.18% versus 0.34% for *Cytb*) and structure in *N. devius* (Fig. 3; Supplementary Data SD1). Almost all haplotypes were shared among ranges, although two occurring at very low frequencies were endemic, one to the western Talamanca site and the other to Tilarán (Fig. 3). As in *R. creper*, F_{ST} and uncorrected *p*-distance values did not show any clear geographic pattern, commonly being higher for pairwise comparisons within ranges than among them. However, one minor result was also consistent with the divergence observed in the mitochondrial marker of this species: highest *p*-distance values were always present in comparisons that involved the western Talamanca site (0.20–0.26%, versus 0.14–0.19% in the rest; Supplementary Data SD1).

Prediction 2—genetic diversity within populations has been affected by both the degree of environmental suitability and its stability through time—was moderately supported by data from the mitochondrial marker of this species (Fig. 4B). Three main populations were also delimited for this rodent, although their geographic compositions differed from those for *R. creper*. One population encompassed all sites from the Tilarán and Central Ranges (the Tilarán–Central population), whereas two others corresponded to the Talamanca Range (western and eastern Talamanca populations). According to the overlapped predictions of suitability across time, these three populations are found in areas where refugia prevail (although note the suitability decrease in Tilarán). In particular, optimal refugia occur across all inhabited ranges, leading to the expectation that all three populations should have remained large and stable. This inference was mostly supported for the western Talamanca population, which had a contextually high haplotype and nucleotide diversity, and for which genetic statistics did not reject a constant population size ($P > 0.775$). The expectations for optimal refugia were only partially met for the other two populations. Genetic statistics did not reject constant population size for the Tilarán–Central population ($P > 0.107$), but one statistic did reject it for the eastern Talamanca population ($P = 0.035$–0.106; Fig. 4B). Additionally, for both these populations, the contrast between haplotype and nucleotide diversity did suggest population expansion, not matching expectations for refugia (Fig. 4B). These molecular results still held when analyzing each sampled site (i.e., mountain peak) as a separate population (Supplementary Data SD1).

Discussion

Considering different levels of suitability in phylogeographic inferences.—The potential advantages of considering different levels of suitability were manifested in at least three notable aspects. First, for both species, the two categories of suitability (optimal or sufficient) yielded opposite predictions of potential connectivity, with patterns observed in the molecular data supporting only one of them. A scenario of isolated populations in optimally suitable environments was supported for the species most restricted to highlands (*R. creper*), whereas a scenario of connected populations in sufficiently suitable environments was supported for *N. devius.* Whereas these differences may stem from limitations inherent to the scaling of model outputs (Phillips et al. 2017), or to our thresholding criteria, the emerging lesson is that a single threshold would have obscured inferences regarding past environmental effects in one of the species. When sufficient molecular data are available, multiple thresholding criteria may be used to yield and test alternative phylogeographic hypotheses under a statistical framework (Galbreath et al. 2010; Demos et al. 2014). Second, for both species, the overall extent of suitable areas did not vary substantially between the climatic extremes considered. Nevertheless, despite apparent stasis of suitable areal extents overall, changes in the particular distributions of patches of categorical levels of suitability are still possible, as was evident for *R. creper* (Fig. 4A). Such a case might be common for tropical montane species, where environmental shifts manifest in elevation rather than latitude. Due to the conformation of mountain ranges, such shifts may implicate only small changes in suitability extent. The increase in categorical suitability and matching signature of population expansion retrieved for *R. creper* illustrates this aspect. Had we not taken into account changes in categorical suitability, the molecular data would have seem at odds with spatial inferences of refugia stable in their extent. Third, and perhaps most importantly, applying different levels of suitability allows finer predictions of population demography in environmental refugia. The advantage of such a finer characterization of refugia was evident in both species, but especially so in *R. creper*, where the degree of suitability varied most across time.

Whereas the relationship between suitability outputs of niche models and population demography needs to be further assessed (Weber et al. 2017; Osorio-Olvera et al. 2019), we propose that different levels of suitability can affect genetic divergence in at least two ways. First, connectivity among populations may cease completely due to the inability of populations to persist in, or individuals to disperse through, unsuitable environments. Second, assuming that the degree of suitability indeed affects local population sizes, it will also affect the number of individuals dispersing into neighboring populations, and consequently, the likelihood of fixation of particular genetic variants. For instance, in this study, population sizes are expected to be highest at the mountain peaks, where optimally suitable environments occur. These populations may exchange individuals via the lower passes separating them, but local densities will be lower there due to poor suitability. Smaller populations yield fewer dispersing individuals; so, even if a haplotype endemic to one mountain peak eventually succeeds in dispersing to another, via intervening populations in suboptimal environments, it will be carried by few individuals. Assuming that natural selection is not occurring, alleles of dispersing individuals tend to have a small probability of fixation, and this will be further reduced if only few individuals disperse, and if they arrive at optimal environments with large populations (i.e., due to genetic swamping—Holt 1996; Kawecki 2008).

Connectivity within tropical montane ecosystems during the Late Quaternary.—Ancestral connectivity, followed by moderate to high isolation in the present, is supported for both species. Although the causes behind these current phylogeographic patterns and the time at which they occurred remain unknown, the predictions of niche models show how past climatic oscillations of the Quaternary are likely candidates. In particular, predictions of niche models for both species support the idea that the way in which past climates affected these tropical montane mesic species was different (indeed opposite) to that of lowland tropical taxa (e.g., Carnaval et al. 2009) or typical temperate species (e.g., Waltari et al. 2007). In general, it appears that taxa inhabiting tropical montane mesic habitats in this region probably experienced more extensive distributions and higher potential for connectivity during the cooler and longer-lasting glacials, retracting and becoming fragmented during the warmer interglacials—a pattern similar to that of species currently inhabiting polar latitudes or temperate montane peaks (Galbreath et al. 2010; Stewart et al. 2010). Such a general pattern seems to be emerging for mesic montane ecosystems along the Neotropics (Amaro et al. 2012; Ramírez-Barahona and Eguiarte 2014; Leite et al. 2016; Paz et al. 2018).

Similar to other studies, these results suggest that the two montane species behaved individualistically in response to common environmental shifts (Demos et al. 2014; Paz et al. 2015). In agreement with the literature regarding their natural history and distributional patterns, niche models suggest that these rodents differ in their environmental associations (McCain 2004, 2006; Reid 2009) and consequently the effects that climatic changes during the Quaternary likely had on their demography. In general, it seems that *R. creper* has been more restricted to higher montane habitats. As such, this species likely has been confined to refugia existing at high elevations during the present interglacial, especially so during the mid-Holocene. Additionally, differences in suitability among these refugia, and in their stability across time, suggest that different demographic processes would be occurring in each of these areas (Figs. 2 and 4A). In general, these spatial inferences are supported by the genetic signatures present in the mitochondrial marker. In particular, the geographic endemicity of mitochondrial haplotypes is striking for this species, especially among the different peaks of the Central Range, where the lower passes separating them are as narrow as 4–8 horizontal km (Figs. 2 and 5A). On the other hand, the suggested increase in suitability during the mid-Holocene for the eastern areas of the Talamanca Range, where there was also a genetic signature of expansion, reiterates the potential idiosyncratic responses regarding the effect of past climate fluctuations in such topographically complex systems.

In contrast, the additional affinity of *N. devius* to lower-elevation montane habitats has apparently rendered past climatic fluctuations less important in shaping current phylogeographic patterns. Overall, niche models for this species indicated the potential for connectivity among populations to be greater and more stable through time (Figs. 3 and 4B). This was supported by the lower levels of genetic structure and divergence observed in the mitochondrial marker (especially among peaks of the Tilarán and Central Ranges), as well as the tests for the genetic statistics, which in general did not reject stable population sizes. Nevertheless, some of the data for this marker do not support the predictions of widespread connectivity and stability derived from the niche models. For instance, most of the haplotypes found at Talamanca were endemic, and the low nucleotide diversity but high haplotype diversity observed at most sites is a pattern typically present in populations that have recently expanded (Milá et al. 2000; Nuñez et al. 2011). This lack of congruence between molecular and spatial data may indicate that: 1) predictions of past suitability are deficient for this species; or 2) additional factors shaped its recent phylogeography in an otherwise extensive and stable suitable region.

Some of the differences in the phylogeographic patterns retrieved for these species might be due to limitations inherent to the data and methodologies employed. Regarding niche models, the biological meaning of suitability outputs, as well as the means of scaling and thresholding them, are still areas in need of much research (Liu et al. 2005; VanDerWal et al. 2009; Phillips et al. 2017). Extrapolation issues and inaccuracies in the paleoclimatic reconstructions may also compromise predictions of suitability during the past (Varela et al. 2015; Guevara et al. 2018a, 2018b). Regarding the molecular data, these species might differ in important aspects of their life history attributes (mostly unknown for tropical species), which can have important effects on genetic patterns (e.g., differences in generation turnover, home ranges, metabolism, sex-biased dispersal, and mutation rates—Brown et al. 2004; Ballard and Rand 2005; Angilletta et al. 2006; Porter and Kearney 2009). Ultimately, divergence rates observed in this study are contingent upon the unknown age at which ancestral lineages colonized the region (Galbreath et al. 2010). Time-calibrated phylogenies and fossil data would help elucidate when colonization and extinction events actually took place in these taxa (e.g., Thomé et al. 2010; Hornsby and Matocq 2012).

Common patterns across montane species of the Talamancan Province.—Besides supporting individualistic species-specific responses to climate change (Stewart et al. 2010; Demos et al. 2014; Paz et al. 2018), the comparative approach employed here also allowed detection of patterns that might be common across other montane taxa within this region. For instance, there seems to be an important genetic break for both species between the Central and Talamanca ranges despite constant presence of sufficiently suitable areas between them according to the niche models. This break may be associated with the lower suitability of the intervening area, or with additional factors not reflected in past climatic reconstructions (e.g., intense volcanic activity and orogenesis at this site during that time period—Vargas Ulate 2009).

Another phylogeographic break observed in both species, although substantially less so for *R. creper*, was that between the western and eastern ends of Talamanca, supported by niche models of both species. Interestingly, divergence between populations on either side of this break was also found in two species of montane rodents of the genus *Scotinomys* (Campbell et al. 2010), as well as in a species complex of a highland anuran (*Craugastor podiciferus*—Streicher et al. 2009). Whereas such a break could result from geographic isolation by distance, niche models for both species also elucidate a specific area (roughly in the middle of this mountain range) that might act as a consistent environmental barrier for montane taxa (Figs. 2 and 3).

Finally, for both species, several peaks within the geologically young Guanacaste Range are suggested to hold at least some suitable areas during most time periods analyzed, especially for *N. devius*; nevertheless, they are also predicted as isolated from known populations (Figs. 2 and 3). Indeed, most of these mountaintops currently exhibit the typical cloud forest habitat in which both species are commonly encountered, although restricted to narrow elevational bands (Nadkarni and Wheelwright 2000; Vargas Ulate 2009). Neither of the focal species has been collected by the sampling carried out on some of these mountains to date, including two expeditions at Tenorio Volcano led by MS-G (see also Anderson and Timm 2006 for inventories on other Guanacaste volcanoes). If the absence of these species from this range is not an artifact of sampling, it appears likely that neither of them has been able to colonize it. Alternatively, these mountains might have been colonized during previous glacials, with local populations becoming extinct during current or past interglacials if suitable areas became very small or nonoptimal (e.g., Colwell and Rangel 2010).

Conclusions and future directions.—This and other studies of tropical montane taxa support the notion that past climatic fluctuations affected population connectivity and divergence in these regions. Nevertheless, it remains to be assessed how these population-level processes led to the remarkable species-level divergence associated with "sky islands" in these regions (Janzen 1967; Weir 2009; Cadena et al. 2012; Fjeldså et al. 2012). Widespread connectivity during cooler conditions implies that connectivity rather than isolation would have prevailed for these taxa during the Quaternary, a time dominated by longer-lasting glacial phases (Colwell and Rangel 2010; Stewart et al. 2010; Leite et al. 2016). In this sense, it is likely that the differing magnitude and duration of glacial phases (Webb and Bartlein 1992; Petit et al. 1999; Jouzel et al. 2007) allowed for any incipient population-level divergence to be maintained across cycles. Similarly, finer temporal variations punctuating glacial phases might have restricted connectivity to only particular time periods; for instance, high humidity levels occurring only during glacial maxima (Auler et al. 2004; Bush et al. 2009).

Beyond improving our understanding of how climatic oscillations of the Quaternary likely affected mesic montane tropical taxa, this study demonstrates how phylogeographic studies stand much to gain from considering more detailed predictions of connectivity and finer characterizations of refugia, including how these change through time. The comparative approach employed revealed individualistic patterns for each species, likely stemming from their specific environmental requirements. Given the stark elevational zonation of endemic taxa in the Talamancan Province, this region represents a fortuitous system for inferring both common and individualistic responses of species to climate change (Colwell and Rangel 2010; Stewart et al. 2010). We hope that this study serves as a baseline and spark for studies harnessing a rich variety of information from niche models to provide a more detailed and realistic understanding of how past climatic fluctuations influenced current biodiversity patterns in many kinds of systems across the world.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Additional methodological details and results for ecological niche models and molecular data.

Supplementary Data SD2.—Occurrence data and spatial groups for *k*-fold cross-validation approach.

Supplementary Data SD3.—GenBank accession numbers for sequences generated in this study.

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APPENDIX I

Gazetteer and Specimens Examined

Specimens of *Nephelomys devius* and *Reithrodontomys creper* examined from Costa Rica and Panama. These correspond to previously collected specimens and those deriving from our own fieldwork. Collecting localities are ordered alphabetically by country and by province (as reported on the specimen tag); within each province, they are ordered geographically (N–S, then W–E). Localities are written verbatim as on specimen tags, except for the use of all caps or capitalization in abbreviated units, the addition of missing abbreviation periods, and obviously missing accent marks or misspelled geographic names. Other corrections or additions (including elevation and geographic coordinates for newly georeferenced localities) are written within brackets, followed by the corresponding sources where applicable. Elevation is given in meters, and geographic coordinates in degrees and minutes rounded to two decimals. When this information was provided on the specimen tag, but in other units (i.e., in feet or decimal degrees), we report the converted data but also give the original information within brackets (conversions to meters were rounded to the nearest multiple of five). Additionally, localities having the same geographic coordinates are listed together. In these cases, we provide the most intuitive description first, followed by the rest of localities within brackets, separated by the = symbol. If the elevation recorded for such grouped localities was different from that provided for the main locality, it is also given (i.e., otherwise it is the same or was absent from the specimen tag and assumed to be similar). For each georeferenced locality, boldface type indicates the information to which the coordinates pertain; localities where coordinates were obtained with GPS by the collector are not bolded. Geographic coordinates for georeferenced localities have an estimated error of 0.5–5 km, usually being < 2 km (details provided in the Supplementary Data SD1). Museum catalog numbers for specimens examined follow each locality, using the following abbreviations. **AMNH:** American Museum of Natural History, New York; **FMNH:** Field Museum, Chicago (formerly Field Museum of Natural History); **KU:** University of Kansas Natural History Museum, Lawrence; **LACM:** Natural History Museum of Los Angeles County, Los Angeles; **LSUMZ:** Louisiana State University Museum of Natural Science, Baton Rouge (formerly LSU Museum of Zoology); **MNCR:** Museo Nacional de Costa Rica, San José; **MSB:** Museum of Southwestern Biology, University of New Mexico, Albuquerque; **MZUCR:** Museo de Zoología, Universidad de Costa Rica, San José; **ROM:** Royal Ontario Museum, Toronto; **UMMZ:** University of Michigan Museum of Zoology, Ann Arbor; **USNM:** United States National Museum of Natural History, Washington, DC. For specimens collected in our field work, we provide the field catalog numbers, denoted by the initials **MSG** or **RPA**. These specimens are now cataloged at the AMNH, MNCR, or MZUCR. * Localities from where tissue samples were obtained. † Locality for which the molecular data was included in the haplotype network (Fig. 2) but excluded from the population genetic analyses due to potentially high georeferencing error (< 10 km). GenBank accession numbers for the sequences generated in this study can be found in the Supplementary Data SD3.

Nephelomys devius (total 290)

COSTA RICA (total 154)

Alajuela

1. *Monteverde; Monteverde Cloud Forest Reserve; **Cerro Amigos; Caribbean Slope, 1750 m** [10°19.08’N, 84°47.54’W; IGNCR, 1966; McCain, 2004; GE, 2013], KU 160983, 160984.
2. *Monteverde; Monteverde Cloud Forest Reserve; **Cerro Amigos, 1750–1840 m** [= Puntarenas, Cerro Amigos, 1840 m; = Puntarenas, Monteverde, Cerro Amigos 1760–1800 m; = Puntarenas, Monteverde; Cerro Amigos; Puntarenas-Guanacaste Border, 1790 m], [10°19.05’N, 84°47.63’W; IGNCR, 1966; McCain, 2004; GE, 2013], FMNH 128415, 128466–128470, KU 143404, 143405, 159043, 159044, 160221, 160222, 160961, MNCR 841.
3. Monteverde; Monteverde Cloud Forest Reserve; **Sendero Pantanosa [Pantano], 1580 m** [10°18.03’N, 84°46.98’W; IGNCR, 1966; GE, 2013], KU 143401.
4. Monteverde; Monteverde Cloud Forest Reserve; **Camino a Peñas Blancas, 1000–1050m** [= Monteverde; Monteverde Cloud Forest Reserve; Peñas Blancas Trail to Refugio Alemán], [10°17.99’N, 84°45.04’W; IGNCR, 1966; McCain, 2004; GE, 2013], KU 159050–159052, 160985.

5. Monteverde; Monteverde Cloud Forest Reserve; **Camino a Peñas Blancas, 1250–1300 m** [= Monteverde; Monteverde Cloud Forest Reserve; Sendero a Peñas Blancas], [10°17.48'N, 84°46.37'W; IGNCR, 1966; McCain, 2004; GE, 2013], KU 159045–159048, 160982.
6. Laja Villa Quesada [**San Juan de Lajas, San Carlos, ca. 1500 m**, 10°15.10'N, 84°24.85'W; C. F. Underwood field notes, 1941; IGNCR, 2004b; GE, 2013], AMNH 139764.
7. **Palmira de Zarcero, 2135 m** [7000 ft, 10°12.71'N, 84°22.75'W; IGNCR, 2004b], FMNH 43998, 43999.
8. *Volcán Poás; 4.6 km NW Poasito; Laguna Botos, 2550 m, 10°11.36'N, 84°13.65'W, MSG 113–115.
9. *Volcán Poás; 5 km NW Poasito, 2500 m, 10°10.99'N, 84°14.30'W, MSG 089, 098, 107.
10. **Volcán Poás Hwy., Río Poasito, 2000 m** [10°09.84'N, 84°12.47'W; P. Myers field notes, 1975; IGNCR, 2005], UMMZ 115422, 123381–123383.

CARTAGO

11. Río Birrís, 12 km N (by road) Portrero [Potrero] Cerrado, 2800 m [9°57.43'N, 83°50.62'W; IGNCR, 1981], ROM 97316, 97317.
12. *Volcán Irazú; 4.6 km N Tierra Blanca, 2650 m, 9°57.29'N, 83°53.07'W, MSG 136, 139, 140, RPA 389, 391.
13. Tapantí, Orosi, **Puente Negro** [ca. 1050 m, 9°48.41'N, 83°51.96'W; GE, 2013], MZUCR 1241, R-19, R-121.
14. **El Muñeco, Río Navarro, 1220–1370 m** [4000–4500 ft, 9°47.61'N, 83°54.62'W; IGNCR, 1963], UMMZ 67290–67297.
15. **Río Macho,** Tapantí, **1300 m** [9°46.68'N, 83°51.36'W; IGNCR, 1963], MZUCR 1706.
16. **Estrella de Cartago,** 1220–1370 m [4000–4500 ft, 9°46.66'N, 83°57.70'W; IGNCR, 1963], UMMZ 64108, 64111, 64123, 64134–64141.
17. Tapantí, Orosi de Paraíso (**RNVS [Refugio Nacional de Vida Silvestre] Tapantí**]) [ca. 1280 m, 9°45.63'N, 83°47.06'W; IGNCR, 1963; GE, 2013], MZUCR R-34, R-38, 1463 (M-2).
18. **Refugio Nacional de Fauna Silvestre Tapantí,** Area B, **near Río Dos Amigos** [= Refugio Nacional de Fauna Silvestre Tapantí], [ca. 1615 m, 9°41.94'N, 83°47.00'W; N. Woodman, in litt.; IGNCR, 1963; GE, 2013], KU 142137, 142142.
19. Upper Río Macho Watershed, **Villa Mills**; Cordillera De Talamanca, 2750 m [= Cordillera de Talamanca, Villa Mills; = Villa Mills. Proyecto CATIE, 2700 m; = Villa Mills; Upper Río Macho Watershed], [9°33.70'N, 83°42.62'W; IGNCR, 1969a], FMNH 123996, KU 143311, 143316, MNCR 848, USNM 565819.

HEREDIA

20. **3 km S, 11 km E de San Miguel.** Parque Nacional Braulio Carrillo, **1080 m** [= Park Nac. Braulio Carrillo, 3.5 km S, 11.5 km E, San Miguel, 1000 m], [10°14.44'N, 84°03.65'W; Timm et al. 1989; IGNCR, 2004a], FMNH 128462, MNCR 845.
21. **5 km E, de Vara Blanca.** Parque Nacional Braulio Carrillo, **2050 m** [= Park Nac. Braulio Carrillo, 5 km E, Vara Blanca], [10°N 10.72', 84°06.85'W; Timm et al. 1989; IGNCR, 2004a; IGNCR, 2005], FMNH 128464, MNCR 842.
22. *Volcán Barva; 13 km N Barva, 2600 m, 10°08.18'N, 84°07.25'W, MSG 015.
23. *Volcán Barva; 13 km N Barva; Laguna del Barva, 2800 m, 10°08.00'N, 84°06.36'W, MSG 002, 011, RPA 361.
24. *Volcán Barva; 12 km N Barva, 2550 m, 10°07.99'N, 84°07.27'W, RPA 370.
25. *Volcán Barva; 12 km N Barva, 2500 m, 10°07.81'N, 84°07.52'W, MSG 004, 010.
26. **10 km NNE Heredia, Cerro Champipe [Chompipe], 2000 m** [10°05.22'N, 84°04.46'W; E. T. Hooper field notes, 1968; IGNCR, 2005], UMMZ 116379, 116380.

LIMÓN

27. **Río Teribe, Valle El Silencio**, 2440 m [8000 ft, 9°6.80'N, 82°57.80'W; IGNCR, 1969b], USNM 539894.

PUNTARENAS

28. **Quebrada Cuecha, Monteverde** [ca. 1530 m, 10°18.37'N, 84°47.74'W; IGNCR, 1966; GE, 2013], USNM 565818.
29. Monteverde; Monteverde Cloud Forest Reserve; **Sendero Chomogo, ~1660 m** [10°18.88'N, 84°46.89'W; IGNCR, 1966; GE, 2013], KU 143402.
30. Monteverde, (**Quebrada Maquinera [Maquinaria]), 1450 m** [10°18.67'N, 84°48.46'W; IGNCR, 1966; GE, 2013], ROM 97301.
31. **Monteverde; Campbell's Woods, 1500 m** [= Monteverde; near Preserve, 1580 m; = Monteverde; W. James house; = Guanacaste, Monteverde, Campbell Woods, 1540 m], [10°18.00'N, 84°48.00'W; IGNCR, 1966; Anderson and Timm, 2006; GE, 2013], KU 143655, LACM 67457, 64850, 64852.
32. Monteverde; **Guindon** Farm, **1510–1520 m** [= Monteverde, 1600 m; = Monteverde; Monteverde Cloud Forest Reserve, 1580 m], [10°17.83'N, 84°47.27'W; IGNCR, 1966; GE, 2013], KU 143403, LACM 64851, 67449, MNCR 1443.
33. *Reserva Bosque Nuboso Monteverde, **0.5 Km Below The Ventana** [= Monteverde; Monteverde Cloud Forest Reserve; Brillante Trail, 1500–1560 m], [ca. 1580 m, 10°17.63'N, 84°46.99'W; IGNCR, 1966; McCain, 2004; GE, 2013], KU 160956–160960, USNM 559053.
34. *Monteverde; Monteverde Cloud Forest Reserve; **Investigator Trail, 1550 m** [10°17.59'N, 84°46.83'W; IGNCR, 1966; McCain, 2004; GE, 2013], KU 159000–159003.
35. **Protrero [Potrero] Grande, Tres Colinas, 1915 m** [9°7.53'N, 83°3.97'W; IGNCR, 1964; GE, 2013], LSUMZ 15808– 15810.

36. San Vito; Coto Brus; **Estación Biológica Las Alturas** [ca. 1450 m, 8°56.72'N, 82°50.00'W; C. McCain personal commun.; R. Timm, in litt.], KU 158634.

San José

37. **0.5 km N (by road) El Empalme, 2208 m** [9°44.13'N, 83°57.10'W; IGNCR, 1963], LSUMZ 29266.
38. **Cerro Estaquero, 3050 m** [10000 ft; = Cartago, Cerro Estaquero, ca. 9700 ft (Cerro de la Muerte)], [9°36.28'N, 83°46.00'W; IGNCR, 1962], LSUMZ 13177, 13178.
39. 4 km S, 2 km E, Ojo de Agua, 2440 m, 9°34.75'N, 83°48.10'W [9.5792°N, 83.8017°W], FMNH 128573.
40. **San Gerardo [de Dota], 2500 m** [9°33.87'N, 83°47.73'W; GE, 2013], MNCR 840, 843, 844.
41. **Estación Biológica Cuericí** [ca. 3000 m, 9°33.70'N, 83°39.70'W; R. Timm personal commun.], KU 158327.
42. *San Gerardo de Dota; El Manantial Lodge, 2300 m, 9°33.58'N, 83°48.38'W, MSG 021–024, 030–032, 036, 038, 039.
43. Finca Montaña Fría. Zapotal, Providencia, 1800 m, 9°31.99'N 83°50.10'W [9.5331°N, 83.8350°W], MNCR 1354, 1356, 1375.
44. Finca Montaña Fría, Zapotal, Providencia, 1950 m, 9°31.87'N, 83°49.81'W [9.5311°N, 83.8301°W], MNCR 1213.
45. **Cerro de la Muerte, 6.8 mi. S "La Georgina", 2500 m** [8200 ft, 9°31.79'N, 83°41.89'W; IGNCR, 1969a], LACM 25432.
46. Río Savegre, Providencia, Toma I, 1450 m [= Toma I. Río Savegre, Providencia], 9°31.60'N, 83°51.65'W [9.5267°N, 83.8608°W], MNCR 1200, 1208, 1209, 1320, 1347, 1348, 1394.
47. **División,** 2300 m [9°30.68'N, 83°42.71'W; IGNCR, 1969a], LSUMZ 28349.
48. **12.5 m. [miles] N of San Isidro [del General] on Pan. Hgwy [Pan American Highway],** 1770 m [5800 ft; = 9 mi N San Isidro del General (Pan. Am. Hwy.) 4800 ft], [9°28.37'N, 83°41.43'W; IGNCR, 1982], LACM 25423, UMMZ 112278.
49. Fila la Máquina, **ca. 3 km E Canaan, 2010 m** [6600 ft, 9°27.09'N, 83°34.67'W; IGNCR, 1982], LSUMZ 13170, 13176.
50. La Piedra, **ca. 4.5 km SW Cerro Chirripó, 3050 m** [10000 ft, 9°26.52'N, 83°31.72'W; A. Gardner, in litt.; GE, 2013], LSUMZ 13179.

PANAMA (total 136)

Bocas del Toro

51. **Upper Río Changena, Rancho Mojica, ca. 20 Mi SSW Changuinola, 1465 m** [4800 ft; = Upper Río Changena, Rancho Caballero, ca. 20 Mi SSW Changuinola, 5000 ft], [8°59.88'N, 82°39.72'W; S. Lotzkat, in litt.; contra Fairchild and Handley, 1966], USNM 319308–319315, 319343.
52. **Boquete, NE, Near Río** Cylindro [Cilindro], **1950 m** [6400 ft, 8°51.07'N, 82°21.50'W; IGNCR, 1964; GE, 2013], USNM 516672–516677, 516679–516681, 516683–516690.
53. **San Félix (Chiriquí), 25 km NNE, 1425–1500 m** [8°29.22'N, 81°46.15'W; R. H. Pine field notes, 1980; GE, 2013], USNM 541119–541144, 541146, 541147, 541157–541160, 541189–541198.

Chiriquí (and Ngöbe Buglé)

54. **El Volcán, 17 Km NNW, Head of Río Candela** [= Río Candela, Headwaters], [ca. 1950 m, 8°54.54'N, 82°43.25'W; AMS, 1964; GE, 2013], USNM 396531, 396532, 516691–516702.
55. *Las Nubes Ranger Station, 2223 m, 8°53.70'N, 82°37.01'W [8.8950°N, 82.6169°W], MSB 262205.
56. *Las Nubes Ranger Station, 2214 m, 8°53.61'N, 82°36.95'W [8.8936°N, 82.6158°W], MSB 261923, 261937, 262150, 262155, 262157.
57. *Las Nubes Ranger Station, 2167 m, 8°53.57'N, 82°36.83'W [8.8928°N, 82.6138°W], MSB 262094.
58. *Las Nubes Ranger Station, 2141–2146 m, 8°53.51'N, 82°36.77'W [8.8918°N, 82.6128°W], MSB 262113, 262135, 262262.
59. **El Volcán, 15.5 km NW, Osta [Santa] Clara, 1700–2200 m** [8°53.12'N, 82°44.36'W; AMS, 1964; GE, 2013], USNM 516682, 516703–516705, 520715.
60. **Cerro Punta,** Above Martinz [Martínez] Dairy, **2075 m** [6800 ft, 8°51.32'N, 82°33.18'W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 314342, 314343.
61. **Cerro Punta, Boquete Trail, 2060–2165 m** [6750–7100 ft, 8°51.30'N, 82°33.18'W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM, 323906, 323910, 323911.
62. **Cerro Punta, Boquete Trail, 2195 m** [7200 ft, 8°50.91'N, 82°32.66'W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 323898, 323899, 323905, 323907, 323909.
63. **Río Chiriquí Viejo, 1700–1720 m,** [8°50.90'N, 82°35.84'W; E. Hooper field notes, 1969; AMS, 1964], UMMZ 116926, 116928–116930.
64. Volcán de Chiriquí, **0.5 miles SE Cerro Punta (town), 2000 m** [8°50.89'N, 82°34.16'W; AMS, 1964], UMMZ 116931.
65. **Cerro Punta**, Behind Casa Tilley, **1615 m** [5300 ft, 8°50.78'N, 82°36.09'W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 314341.
66. **Cerro Punta, Boquete Trail, 2285–2380 m** [7500–7800 ft, 8°50.6'N, 82°31.97'W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 318427, 318428, 323900–323904, 323908.
67. **Río Chiriquí Viejo, 1600 m** [8°50.25'N, 82°36.59'W; E. Hooper field notes, 1969; AMS, 1964], UMMZ 116927.

68. **Boquete, 1830 m** [6000 ft, 8°46.71’N, 82°23.69’W; AMS, 1959], FMNH 18872, 18873, USNM 243412.
69. Chiriquí-Bocas del Toro boundary, **Cerro Bollo, 3.5 km E Escopeta**, which latter is ca. 23 km NNE San Felix, **1800–1856 m** [= Chiriquí-Bocas del Toro boundary, 3.5 km E Escopeta Camp, which latter is 23 km NNE San Félix; = Chiriquí-Bocas del Toro boundary, 3.5 km E. Escopeta Cerro Bollo, which former is 23 km NNE San Félix], [8°29.69’N, 81°45.53’W; R. H. Pine field notes, 1980; GE, 2013], USNM 541145, 541148, 541150–541154; 541199.
70. **24 km NNE San Félix (Chiriquí), 1275–1325 m** [= 24 km NNE, Near Escopeta Camp], [8°28.56’N, 81°46.07’W; R. H. Pine field notes, 1980; GE, 2013], USNM 541155, 541156, 541161.

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COSTA RICA (total 176)

Alajuela

1. *Volcán Poás; 4.6 km NW Poasito; Laguna Botos, 2550 m, 10°11.36’N, 84°13.65’W, MSG 111, 116.
2. **Volcán Poás, 2540 m** [10°11.13’N, 84°14.34’W; IGNCR, 2004a], MNCR 1431.
3. *Volcán Poás; 5 km NW Poasito, 2500 m, 10°10.99’N, 84°14.30’W, MSG 090, 091, 097, 105, 119.
4. *Volcán Poás; 5 km NW Poasito, 2500 m, 10°10.68’N, 84°14.21’W, MSG 103, 104, 108.
5. **Volcán Poás Hwy., 2400 m** [= Volcán Poás, 7900 ft], [10°9.93’N, 84°13.90’W; IGNCR, 2005], LSUMZ 11519, 11520, UMMZ 115440, 115441.
6. **Volcán Poás Hwy., Río Poasita [Río Poasito], 2000 m** [= Volcán Poás, Río Poasito], [10°9.84’N, 84°12.47’W; P. Myers field notes, 1975; IGNCR, 2005], UMMZ 115439, 123360.

Cartago

7. **Volcán Turrialba Had. [Hacienda el Retiro], 2590 m** [10°0.87’N, 83°47.36’W; E. Hooper field notes, 1969; IGNCR, 1967], UMMZ 116886.
8. Volcán Irazú, **~1 km below crater** by rd., 3300 m [9°58.72N, 83°50.30’W; GE, 2013], UMMZ 123354–123357.
9. **Volcán Irazú, Hwy. Rt. 8, 3180–3200 m** [9°58.59’N, 83°49.86’W; IGNCR, 1981], UMMZ 112146–112154.
10. **Volcán Irazú, 2970 m** [9°57.84’N, 83°49.82’W; M. Engstrom in litt.; GE, 2013], MNCR 1429, 1430.
11. *Volcán Irazú; 5.3 km N Tierra Blanca, 2825 m, 9°57.59’N, 83°52.54’W, RPA 392.
12. **Volcán Irazú 1/8 mi N Hotel Robert, 2850 m** [9°57.50’N, 83°50.73’W; E. Hooper field notes, 1962; IGNCR, 1981], UMMZ 116885.
13. **Rio Birrís, 12 km N (by road) Portrero [Potrero] Cerrado, 2800 m** [9°57.43’N, 83°50.62’W; IGNCR, 1981], ROM 97318–97320, 97322, 97323.
14. *Volcán Irazú; 4.6 km N Tierra Blanca, 2650 m, 9°57.29’N, 83°53.07’W, MSG 138.
15. *Volcán Irazú; 4.5 km N Tierra Blanca, 2650 m, 9°57.22’N, 83°52.89’W, MSG 134.
16. Volcán Irazú, **Finca Coliblanco, 2350 m** [9°57.04’N, 83°48.88’W; E. Hooper field notes, 1962; IGNCR, 1981], UMMZ 112143–112145.
17. **4 km NE Copey** [ca. 2480 m, 9°40.07’N, 83°52.84’W; P. Myers field notes, 1975; IGNCR, 1963], UMMZ 123361, 123362.
18. Pan Am Hway, **Salsipuedes, 2730 m** [9°39.04’N, 83°51.04’W; IGNCR, 1962], UMMZ 123359.
19. **2 km NNW Dos Amigos, Pan Am Hway, 2800 m** [9°38.51’N, 83°50.78’W; IGNCR, 1962], UMMZ 123358, 123393.
20. **1.7 km E Ojo de Agua** [ca. 2920 m; 9°36.97’N, 83°48.14’W; IGNCR, 1962], UMMZ 123363.
21. **N Side Summit, Pan Am Hwy., Cerro de la Muerte, 3110 m** [10200 ft; = San José, Summit, Pan Am Hwy., Cerro de la Muerte], [9°34.70’N, 83°45.46’W; D. J. Klingener field notes, 1962; IGNCR, 1962], UMMZ 112129–112141.
22. **Cerro Asunción, 3355 m** [11000 ft, 9°34.58’N, 83°45.46’W; IGNCR, 1962], LSUMZ 13235–13240.
23. **Cerro de la Muerte, 3335 m** [= Estación Biológica Cerro de la Muerte, 3100 m, 9.5589°N, 83.7611°W; = Estación Cerro de la Muerte. Federico Valverde, 3200 m, 9.5589°N, 83.7611°W], [9°34.00’N, 83°45.00’W; GE, 2013], MNCR 1276, 1339, 1377, UMMZ 115431–115436.
24. **Villa Mills. Proyecto CATIE, 2700 m** [9°34.00’N, 83°41.50’W; IGNCR, 1969a], MNCR 926, 944.
25. Cerro de la Muerte, **Villa Mills,** 3110 m [10200 ft; = ca. 1 km NW Villa Mills], [9°33.71’N, 83°42.63’W; IGNCR, 1969a], LSUMZ 13241, UMMZ 115437, 115438.
26. **Cerro Estaquero** (Cerro de la Muerte), **2955 m** [9700 ft; = San José Province, Cerro Estaquero, 10000 ft], [9°36.28’N, 83°46.00’W; IGNCR, 1962], LSUMZ 13229–13234, 14464, 14465.

Heredia

27. Parque Nacional Braulio Carrillo, **5 km E, Vara Blanca, 2050 m** [= Park Nac. Braulio Carrillo, 5 km E, Vara Blanca], [10°10.72’N, 84°6.85’W; Timm et al. 1989; IGNCR, 2004a; IGNCR, 2005], FMNH 128545–128548.
28. **Volcán Barva, 2800 m** [10°8.08’N, 84°6.60’W; M. Fernández, in litt.; IGNCR, 2005], MNCR 1562–1564.
29. *Volcán Barva; 13 km N Barva; Laguna del Barva, 2800 m, 10°8.00’N, 84°6.36’W, MSG 001, 006, 007, RPA 350, 351.
30. *Volcán Barva; 12 km N Barva, 2500 m, 10°7.81’N, 84°7.52’W, MSG 012, 013.
31. **Río Las Vueltas & Hwy. 113**, **S Fork;** Alto del Roble [= Alto del Roble; S. Fork Río las Vueltas & Hwy. 113], [2030 m, 10°5.35’N, 84°4.14’W; IGNCR, 2005], LACM 26457–26459.

Limón

32. Cotón Drainage [**Río Teribe, Valle El Silencio**], 2440 m [8000 ft, 9°6.80’N, 82°57.80’W; IGNCR, 1969b], USNM 539908–539913.

Puntarenas

33. *Monteverde; **Cerro Amigos**, 1760–1810 m [= Monteverde; Cerro Amigos; Puntarenas-Guanacaste Border], [10°19.05’N, 84°47.63’W; McCain, 2004; GE, 2013], FMNH 128550, KU 142062, 142079–142090, 143425–143431, 143433, 143434.
34. **La Ventana**, Reserva Bosque Nuboso Monteverde [1580 m, 10°17.63’N, 84°46.99’W; IGNCR, 1966; GE, 2013], USNM 559059, 559060.

San José

35. **N.W. slope of Volcan Irazú, above Cascajal (Road to),** property of Hacienda Forestales, **1750 m** [10°0.53’N, 83°57.38’W; IGNCR, 1967], AMNH 249790, 249791.
36. **Cerro Rabo de Mico**, Inventario Cerros de Escazú, **2300 m** [9°50.99’N, 84°8.53’W; IGNCR, 1989], MZUCR 1578.
37. **Canon [Cañón]**, Area B, near Río Dos Amigos, **ca. 2590 m** [~8500 ft, 9°41.11’N, 83°55.29’W; IGNCR, 1963], KU 71311–71314.
38. **Santa María, 1500 m** [9°39.25’N, 83°58.22’W; IGNCR, 1962], MNCR 929.
39. Cerro Buena Vista, Páramo, 3415 m, 9°35.53’N, 83°45.67’W [9.5922°N, 83.7611°W], MNCR 1340, 1357.
40. 4 km S, 2 km E, Ojo de Agua, 2440 m, 9°34.75’N, 83°48.10’W [9.5792°N, 83.8017°W], FMNH 128551, 128552.
41. **San Gerardo de Dota**, **2550 m** [= San Gerardo, 2300–2700 m], [9°34.00’N, 83°48.00’W; GPS by MSG for town plaza at 2100 m], KU 158464, MNCR 413, 927, 928, USNM 559043, 562175.
42. *Cerro de la Muerte; km 92, 3050 m, 9°33.80’N, 83°44.50’W, MSG 046, 052–057.
43. **Estación Biológica Cuericí**, [ca. 3000 m, 9°33.70’N, 83°39.70’W; R. Timm personal commun.], KU 158332.
44. **5.5 mi-Pan Am Hway-S Summit**, La Georgina, [ca. 3000 m, 9°33.59’N, 83°43.52’W; E. Hooper field notes, 1962; IGNCR, 1969a], UMMZ 112126–112128.
45. *San Gerardo de Dota; El Manantial Lodge, 2300 m, 9°33.58’N, 83°48.38’W, MSG 026.
46. **Macizo Buena Vista**. Cerro de la Muerte, 3420 m, 9°33.53’N, 83°45.67’W [9.5589°N, 83.7611°W], MNCR 1312, 1313.
47. La Piedra, **ca. 4 km SW Cerro Chirripó, 3200 m** [10500 ft; = La Piedra, ca. 4.5 km SW Cerro Chirripó, 10000 ft], [9°26.52’N, 83°31.72’W; GE, 2013; A. Gardner personal commun.], LSUMZ 13242, 13244–13248.

PANAMA (total 130)

Bocas del Toro

48. El Volcán, **17.5 Km NNW, NE of Cerro Pando, 1950 m** [6400 ft, 8°55.82’N, 82°41.64’W; AMS, 1964; GE, 2013], USNM 516778–516792.
49. **Boquete, NE, Near Río** Cylindro [Cilindro], **1950 m** [8°51.07’N, 82°21.50’W; IGNCR, 1964; GE, 2013], USNM 516777.

Chiriquí (and Ngöbe buglé)

50. *Las Nubes Ranger Station, 2223 m, 8°53.70’N, 82°37.01’W [8.8950°N, 82.6169°W], MSB 262206, 262213, 262214.
51. *Las Nubes Ranger Station, 2207 m, 8°53.66’N, 82°36.91’W [8.8943°N, 82.6151°W], MSB 261982.
52. *Las Nubes Ranger Station, 2146 m, 8°53.51’N, 82°36.77’W [8.8918°N, 82.6128°W], MSB 262111, 262112, 262272, 262278, 262281.
53. *Las Nubes Ranger Station, 2214 m, 8°53.62’N, 82°36.95’W [8.8936°N, 82.6158°W], MSB 261941, 261943, 262142.
54. Cerro Punta, **Boquete Trail, 2075–2165 m** [6800–7100 ft, 8°51.30’N, 82°33.18’W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 323782, 323783, 323792, 323799, 323804–323806, 323814, 323825–323827, 323832–323834, 323836, 323837.
55. Cerro Punta, **Boquete Trail, 2180–2240 m** [7150–7350 ft, 8°50.91’N, 82°32.66’W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 323784–323788, 323793–323797, 323807–323810, 323816, 323817, 323820, 323821, 323828, 323838–323841, 323843–323845.
56. Cerro Punta, **Boquete Trail, 2315–2380 m** [7600–7800 ft, 8°50.60’N, 82°31.97’W; C. Handley field notes, 1962; AMS, 1964; GE, 2013], USNM 318431–318433, 323789–323791, 323798, 323800–323803, 323811–323813, 323815, 323818, 323819, 323822–323824, 323829–323831, 323835, 323842.
57. El Hato, **Volcán Barú Crater, 3200 m** [10500 ft; = Volcán de Chiriquí; Chiriquí, Potrero, 10200 ft] [8°48.67’N, 82°31.87’W; GE, 2013], UMMZ 95739, 95740, USNM 314778.
58. †***W El Barú, 2350 m** [7700 ft; = Parque Nacional Volcán Barú, Bosque], [8°48.65’N, 82°33.87’W; E. Tyson field catalogue, 1961, 1962; GE, 2013], MSB 130119, USNM 520583.
59. **Escopeta Camp, 3.5 Km E, Cerro Bollo, 1800–1856 m** [= Ciriquí-Bocas del Toro boundary, 3.5 km E Escopeta Camp, which latter is 23 km NNE San Félix, Cerro Bollo], [8°29.69’N, 81°45.53’W; R. H. Pine field notes, 1980; GE, 2013], USNM 541202–541231.