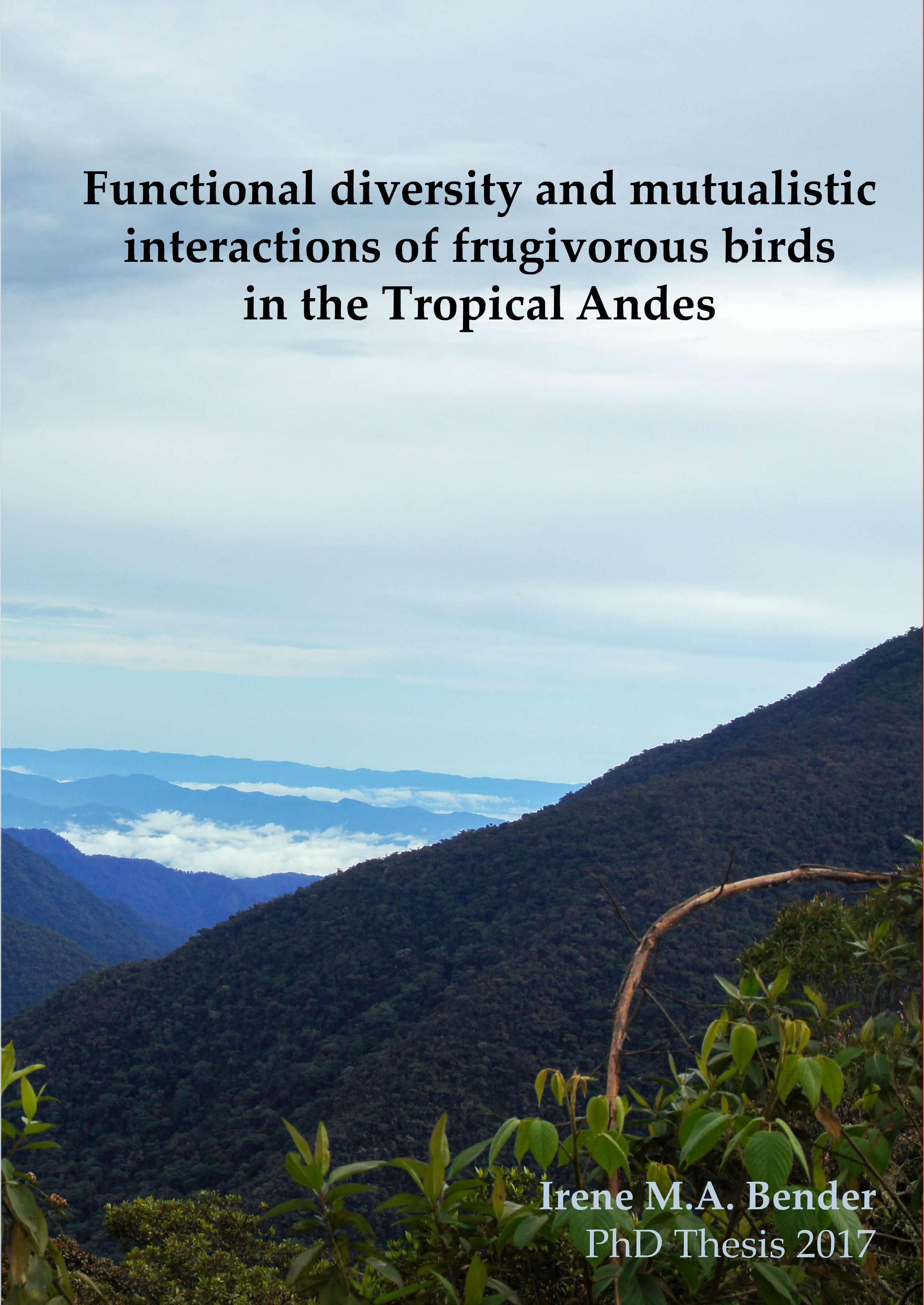
Functional diversity and mutualistic interactions of frugivorous birds in the Tropical Andes



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Functional diversity and mutualistic interactions of frugivorous birds in the Tropical Andes

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To Opa Leo...

...a curious mind never stops wondering
...a scientific mind never stops studying

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Summary

SUMMARY

Interactions between consumer and resource species are organized in complex ecological networks. These interactions are greatly influenced by the functional traits of the interacting species. In mutualistic interactions, such as seed dispersal networks between birds and plants, interactions are mostly determined by the degree of compatibility between the characteristics (morphological traits) of interacting partners. There has been increasing interest in the functional aspects of interaction networks in recent years, especially since the functional diversity of communities also provide insights into the overall functioning of ecosystems. One way to study the functionality of interaction networks is to study the functional role that species fulfill in their community, how functionality varies through space and time, and how it could change in the future.

This PhD thesis aims to improve the current understanding of functional diversity in seed dispersal networks. It covers three studies, which explore the functional diversity of communities from three different perspectives by focusing on seasonal variation, spatial variation, and future projections. Seed dispersal is a crucial ecosystem function, especially in tropical forests where 90% of woody plant species depend on animals for their dispersal. The present thesis focuses on seed dispersal networks across the tropical Andes. The Andes are a particularly important region because it is a biodiversity hotspot for frugivorous birds and fleshy-fruited plants alike.

In the first study, I investigated the effect of seasonal variation in resource availability on the functional diversity of frugivorous birds. I focused on two interaction networks with four temporal replicates from the tropical Andes. The results indicated that even though the types of available fruits changed throughout the year, the degree of functional specialization of bird species remained rather stable. In addition, the degree of functional specialization was positively related to functional flexibility (*i.e.*, the ability of bird species to change their fruit preference across seasons). This indicates that the species with the highest degree of functional specialization were also the species with the highest flexibility to change to alternative resource types. Consumer species' flexibility may be an important mechanism for the stabilization of consumer-resource networks in response to climate change or other drivers of global change.

The second study tested the generality of trait matching in interactions between fleshy-fruited plants and frugivorous birds. To this end, I combined trait data (for plants and birds) and interaction data from eight interaction networks between fleshy-fruited plants and frugivorous birds, sampled across the tropical and subtropical Andean range. The results indicated that traits related to size matching and traits related to animal foraging were equally important for shaping the interactions between Andean plant and bird species. This indicates that morphological trait matching between fleshy-fruited plants and frugivorous birds is a general phenomenon in plant-frugivore networks across the Andes. These results are a first step towards the deduction of general interaction rules based on functional traits. It provides the basis for predicting unknown interactions from species' functional traits in novel ecological communities, *e.g.*, as a result of species migrations and/or local extinctions in response to climate change.

Finally, the third study explored potential changes in functional diversity of frugivore communities by projecting the communities into the future under ongoing anthropogenic climate change. I combined approaches from biogeography and community ecology, and calculated the functional diversity of current and projected future frugivorous bird communities along an elevational gradient in the tropical Andes. The results indicated that communities at different elevations along a tropical mountain might be affected in different ways. Specifically, lowland communities are likely to face a loss of ecological functionality in the future, while communities at mid-elevations are likely to reshuffle, which puts strong pressure on these communities to adapt to changes in community composition. These findings suggest that climate change will be an important factor in shaping the structure of these communities in the future.

Overall, this thesis contributes to our understanding on how species' functional traits define the functional role that species fulfill in a community. I discuss the flexibility of species to shift between resources, the generality of trait matching in interactions networks, and the potential changes in communities' functional diversity under projected climate change. While I focus on the specific mutualistic interactions of seed dispersal in the tropics, the concepts and theory that I discuss are applicable beyond this scope, *e.g.*, in other ecological interactions such as pollination networks. Overall, the results suggest that the functional composition of communities is likely to change considerably in the future. I identified mechanisms that could help to stabilize these communities. For example, functional flexibility of consumer species might help these communities to restructure and persist in the future. The generality of trait matching can aid the identification of interaction rules that can be applied to predict the potential for rewiring in projected future communities. This thesis therefore provides valuable information on how to improve the projections of functional diversity and ecosystem functioning under future conditions.

Zusammenfassung

ZUSAMMENFASSUNG

Interaktionen zwischen Konsumenten- und Ressourcenarten sind in komplexen ökologischen Netzwerken organisiert. Diese Interaktionen werden in hohem Maße von den funktionalen Merkmalen der interagierenden Arten beeinflusst. Bei mutualistischen Interaktionen, wie in Samenausbreitungsnetzwerken zwischen Vögeln und Pflanzen, werden Interaktionen hauptsächlich von dem Grad der Kompatibilität der Charakteristika (morphologische Merkmale) zwischen den Interaktionspartnern bestimmt. In den letzten Jahren gab es ein wachsendes Interesse daran, funktionale Aspekte von Interaktionsnetzwerken zu erforschen, besonders, da die funktionale Diversität von Artengemeinschaften auch Einblicke in das allgemeine Funktionieren von Ökosystemen gibt. Eine Möglichkeit die Funktionalität von Interaktionsnetzwerken zu erforschen ist die funktionale Rolle zu studieren, die Arten in ihrer Artengemeinschaft erfüllen, sowie die Variabilität dieser Rolle in Raum und Zeit und dessen wie sie sich in der Zukunft ändern könnte.

Diese Doktorarbeit hat zum Ziel das aktuelle Verständnis funktionaler Diversität in Samenausbreitungsnetzwerken zu verbessern. Sie umfasst drei Studien, welche die funktionale Diversität von Artengemeinschaften aus drei verschiedenen Perspektiven beleuchten, mit Fokus auf saisonale Variation, räumliche Variation und Zukunftsprojektionen. Samenausbreitung ist eine wichtige Ökosystemfunktion, besonders in tropischen Wäldern, wo 90% der Holzpflanzen in ihrer Ausbreitung von Tieren abhängen. Die vorliegende Arbeit konzentriert sich auf Samenausbreitungsnetzwerke in den tropischen Anden. Die Anden sind eine besonders wichtige Region, da sie gleichermaßen ein Hotspot für die Diversität von fruchtfressenden Vögeln als auch von fleischfrüchtigen Pflanzen sind.

In der ersten Studie habe ich Effekte saisonaler Variation im Ressourcenangebot auf die funktionale Diversität fruchtfressender Vögel untersucht. Ich konzentrierte mich auf zwei Interaktionsnetzwerke aus den tropischen Anden mit je vier zeitlichen Replikaten innerhalb eines Jahres. Die Ergebnisse zeigten, dass auch wenn die verfügbaren Fruchttypen sich über das Jahr veränderten, der Grad der funktionalen Spezialisierung der Vogelarten stabil blieb. Darüber hinaus war der Grad der funktionalen Spezialisierung positiv mit der funktionalen Flexibilität (die Fähigkeit der Vogelarten, ihre Fruchtpräferenzen mit der Saison zu verändern) assoziiert. Das zeigt, dass Arten mit dem höchsten Grad an funktionaler Spezialisierung auch die Arten waren, die am flexibelsten zu alternativen Ressourcentypen wechselten. Diese Flexibilität der Konsumentenarten könnte einen wichtigen Mechanismus zur Stabilisierung von Konsumenten-Ressourcennetzwerken als Reaktion auf den Klimawandel oder andere Faktoren des globalen Wandels darstellen.

Die zweite Studie testete die Allgemeingültigkeit von Merkmalskompatibilität in Interaktionen zwischen fleischfrüchtigen Pflanzen und fruchtfressenden Vögeln, gesammelt in der subtropischen und tropischen Zone der Anden. Die Ergebnisse zeigten, dass Merkmale, die mit der Größenkompatibilität zusammenhängen, dieselbe Bedeutung für das Ausformen der Interaktionen zwischen Pflanzen und Tieren hatten wie Merkmale, die mit

der tierischen Nahrungssuche assoziiert sind. Das deutet darauf hin, dass die morphologische Merkmalskompatibilität zwischen fleischfrüchtigen Pflanzen und fruchtfressenden Vögeln ein allgemeingültiges Phänomen in Pflanzen-Fruchtfresser-Netzwerken in den Anden ist. Die Studie ist ein erster Schritt zur Ableitung von allgemeingültigen Interaktionsregeln, basierend auf funktionalen Merkmalen. Dadurch stellt die Studie eine Grundlage bereit, um unbekannte Interaktionen in neuen Artengemeinschaften anhand funktionaler Merkmale der Arten vorherzusagen.

Die dritte Studie erforschte potentielle Veränderungen in der funktionalen Diversität von Fruchtfresser-Artengemeinschaften, indem die Artengemeinschaften in eine Zukunft unter andauerndem anthropogen verursachten Klimawandel projiziert wurden. Ich kombinierte Ansätze aus der Biogeographie und der Gemeinschaftsökologie und berechnete die funktionale Diversität aktueller und projizierter Zukunftsartengemeinschaften fruchtfressender Vögel entlang eines Höhengradienten in den tropischen Anden. Die Ergebnisse zeigten, dass Artengemeinschaften auf verschiedenen Höhen entlang eines tropischen Berges möglicherweise auf unterschiedliche Art und Weise beeinträchtigt werden. Besonders Artengemeinschaften im Tiefland werden in Zukunft voraussichtlich einem Verlust an ökologischer Funktionalität begegnen. Dagegen werden Artengemeinschaften auf mittleren Höhen vermutlich umstrukturiert, wodurch diese Artengemeinschaften gezwungen sind sich den Änderungen in der Zusammensetzung der Artengemeinschaften anzupassen. Diese Ergebnisse legen nahe, dass der Klimawandel zukünftig ein wichtiger Faktor im Ausformen der Struktur dieser Artengemeinschaften sein wird.

Insgesamt trägt diese Arbeit zum allgemeinen Verständnis bei, wie funktionale Merkmale die funktionale Rolle definieren, die eine Art in der Artengemeinschaft erfüllt. Ich diskutiere die Flexibilität von Vogelarten, um zwischen unterschiedlichen Ressourcen zu wechseln, die Allgemeingültigkeit der Merkmalskompatibilität in Interaktionssystemen und die potentiellen Veränderungen in der funktionalen Diversität von Artengemeinschaften unter einem projizierten Klimawandel. Während ich mich auf mutualistische Samenausbreitungsinteraktionen in den Tropen konzentriere, können die Konzepte und Theorien, die ich diskutiere darüber hinaus in anderen ökologischen Netzwerken angewandt werden, wie zum Beispiel in Bestäubungsnetzwerken. Zusammenfassend legen die Ergebnisse nahe, dass sich die funktionale Komposition der Artengemeinschaften in Zukunft wahrscheinlich stark ändern wird. Ich identifizierte Mechanismen, die eine stabilisierende Wirkung auf die Artgemeinschaften haben könnten. So könnte die funktionale Flexibilität von Konsumentenarten sich unterstützend auf die Restrukturierung von Artengemeinschaften auswirken und damit bereitstellen, dass diese Gemeinschaften auch in der Zukunft bestehen. Die Allgemeingültigkeit der Merkmalskompatibilität kann bei der Identifizierung von speziellen Interaktionsregeln helfen, die wiederum angewendet werden können, um die zukünftig durch den Klimawandel umstrukturierten Artengemeinschaften neu zu vernetzen. Die vorliegende Arbeit stellt daher wertvolle Information bereit, um Zukunftsprojektionen zur funktionalen Diversität und zum Funktionieren von Ökosystemen zu verbessern.

Samenvatting

SAMENVATTING

Interacties tussen consumenten (*e.g.*, dieren) en producenten (*e.g.*, planten) zijn georganiseerd in complexe ecologische netwerken. Deze interacties worden in hoge mate beïnvloed door de functionele eigenschappen van de samenwerkende soorten. In mutualistische interacties, zoals zaadverspreidingsnetwerken tussen vogels en planten, worden interacties vooral bepaald door de mate van compatibiliteit tussen de kenmerken (morfologische eigenschappen) van de samenwerkende partners. Er is de laatste jaren steeds meer belangstelling om de functionele aspecten van interactienetwerken te bestuderen, vooral omdat de functionele diversiteit van gemeenschappen ook inzicht verschaft in het algeheel functioneren van deze ecosystemen. De functionaliteit van interactienetwerken kan worden bestudeerd door te kijken naar de functionele rol die soorten in hun gemeenschap vervullen, naar de variabiliteit hiervan in ruimte en tijd en naar de wijze waarop dit in de toekomst kan veranderen.

Dit proefschrift heeft als doel de huidige kennis van functionele diversiteit in zaadverspreidingsnetwerken te verbeteren. Het omvat drie onderzoeken, die de functionele diversiteit van gemeenschappen bekijken vanuit drie verschillende perspectieven. Deze onderzoeken focussen op seizoensvariatie, ruimtelijke variatie en toekomstprognoses. Zaadverspreiding is een cruciale functie in ecosystemen, vooral in tropische bossen waar 90% van de houtachtige plantensoorten afhankelijk zijn van dieren voor hun verspreiding. Dit proefschrift richt zich op zaadverspreidingsnetwerken in de tropische Andes. De Andes zijn een bijzonder belangrijke regio omdat het een biodiversiteitshotspot is voor zowel vruchtetende vogels als planten met vlezige vruchten.

In het eerste onderzoek bestudeer ik het effect van variatie tussen seizoenen in de beschikbaarheid van voedselbronnen op de functionele diversiteit van vrucht etende vogels. Ik focus op twee interactienetwerken met elk vier seizoens replica's in de tropische Andes. De resultaten tonen aan dat hoewel de beschikbare types fruit het hele jaar door veranderen, de mate van functionele specialisatie van vogelsoorten vrij stabiel blijft. De mate van functionele specialisatie is bovendien positief gecorreleerd aan functionele flexibiliteit (d.w.z. het vermogen van vogelsoorten om hun fruitvoorkeur te veranderen tussen seizoenen). Dit wijst erop dat de soort met het hoogste niveau van functionele specialisatie ook de soort is met de hoogste flexibiliteit om over te stappen naar alternatieve soorten vruchten. Deze flexibiliteit van consumenten kan een belangrijk mechanisme zijn voor de stabilisatie van consument-producent netwerken onder klimaatverandering, of andere oorzaken van wereldwijde verandering.

In het tweede onderzoek test ik in hoeverre de hoge compatibiliteit van eigenschappen in interacties tussen planten met vlezige vruchten en vruchtetende vogels een algemeen voorkomend mechanisme is in de gehele Andes. Hiertoe zijn morfologische eigenschappen (voor planten en vogels) gecombineerd met interactiedata van acht interactienetwerken tussen planten met vlezige vruchten en vruchtetende vogels, verzameld over het tropische

en subtropische deel van het Andesgebergte. De resultaten wijzen er op dat eigenschappen die verband houden met de compatibiliteit van groottes én eigenschappen die verband houden met het foerageren van dieren in gelijke mate invloed hebben op het vormen van interacties tussen planten en vogels. Dit toont aan dat compatibiliteit van morfologische eigenschappen tussen planten met vlezige vruchten en vruchtetende vogels een algemeen verschijnsel is in plant-frugivore netwerken in de Andes. Deze resultaten zijn een eerste stap naar het afleiden van algemene interactieregels gebaseerd op functionele kenmerken. Het biedt de basis voor het voorspellen van onbekende interacties gebaseerd op de functionele eigenschappen van soorten in nieuwe ecologische gemeenschappen, bijvoorbeeld als gevolg van migraties van soorten en/of lokale uitsterving door klimaatverandering.

Het derde onderzoek focust zich op de potentiële veranderingen in functionele diversiteit van gemeenschappen van frugivoren door deze naar de toekomst te projecteren. In deze projecties wordt rekening gehouden met voortdurende antropogene klimaatverandering. Ik heb methodes uit de biogeografie en de gemeenschapsecologie gecombineerd en de functionele diversiteit van huidige en geprojecteerde toekomstige frugivore gemeenschappen langs een verticale gradient in de tropische Andes berekend. De resultaten wijzen erop dat gemeenschappen op verschillende hoogtes in een tropische gebergte op verschillende manieren kunnen worden beïnvloed. Met name laaggelegen gemeenschappen zijn kwetsbaar voor het verlies van ecologische functionaliteit, terwijl gemeenschappen halverwege de berg zich waarschijnlijk zullen herschikken, wat deze gemeenschappen onder druk zet om zich aan te passen aan de veranderingen in de soortensamenstelling. Deze bevindingen suggereren dat klimaatverandering een belangrijke factor zal zijn in het vormgeven van de toekomstige structuur van deze gemeenschappen.

Met deze drie onderzoeken draagt dit proefschrift bij aan de algemene kennis van hoe functionele eigenschappen van soorten de functionele rol definiëren die soorten vervullen in een gemeenschap. Ik bespreek de flexibiliteit waarmee soorten wisselen tussen producenten, de algemeenheid van compatibiliteit van eigenschappen in interactiesystemen en de veranderingen in functionele diversiteit van gemeenschappen onder de verwachte klimaatverandering. Hoewel ik me concentreer op de specifieke mutualistische interacties van zaadverspreiding in de tropen, zijn de concepten en theorieën die ik bespreek ook buiten dit kader toepasbaar, bijvoorbeeld in andere ecologische interacties zoals bestuivingsnetwerken. De resultaten suggereren dat de functionele samenstelling van gemeenschappen in de toekomst aanzienlijk kan veranderen. Ik heb mechanismen geïdentificeerd die deze gemeenschappen kunnen helpen stabiliseren. Functionele flexibiliteit kan deze gemeenschappen bijvoorbeeld helpen om in de toekomst te herstructureren en te blijven bestaan. De algemeenheid van compatibiliteit van eigenschappen kan helpen bij het identificeren van specifieke interactieregels die kunnen worden toegepast om het potentieel voor herschikking in geprojecteerde toekomstige gemeenschappen te kunnen voorspellen. Dit proefschrift biedt daarom waardevolle informatie om de projecties van functionele diversiteit en het functioneren van ecosystemen onder toekomstige omstandigheden te verbeteren.

Resumen

RESUMEN

Las interacciones entre las especies consumidoras y sus especies recurso están organizadas en redes ecológicas complejas. Estas interacciones están fuertemente influenciadas por los rasgos funcionales de las especies que interactúan. En interacciones mutualistas, tales como las redes de dispersión de semillas entre plantas y aves frugívoras, las interacciones están principalmente determinadas por el grado de compatibilidad entre las características (rasgos morfológicos) de las parejas interactuantes. En los últimos años se ha observado un aumento por el interés en el estudio de los aspectos funcionales de las redes de interacciones, especialmente desde que la diversidad funcional de las comunidades proporciona una nueva perspectiva para el entendimiento del funcionamiento global de los ecosistemas. Una forma de estudiar la funcionalidad de las redes de interacción es mediante el análisis del papel funcional que las especies desempeñan en sus comunidades, su variabilidad espacial y temporal, y cómo esto podría cambiar en el futuro.

El objetivo de esta tesis doctoral es mejorar el conocimiento actual sobre la diversidad funcional en redes de dispersión de semillas. Concretamente, abarca tres estudios, los cuales exploran la diversidad funcional desde tres perspectivas diferentes poniendo énfasis en la variación estacional, la variación espacial y las proyecciones de futuro. La dispersión de semillas es una función crucial de los ecosistemas, especialmente en los bosques tropicales donde el 90% de las especies de plantas leñosas dependen de animales para su dispersión. La presente tesis se centra en las redes de dispersión planta-ave frugívora a lo largo de los Andes Tropicales. Los Andes son una región especialmente importante debido a su gran diversidad de aves frugívoras, así como de plantas de fruto carnoso.

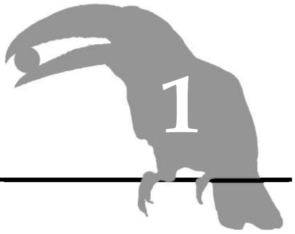
En el primer estudio, investigué el efecto de la variación estacional de los recursos disponibles en la diversidad funcional de las aves frugívoras. Me centré en dos redes de interacciones con cuatro replicas temporales de los Andes tropicales. Los resultados indicaron que a pesar de los cambios que se produjeron a lo largo del año en los tipos de frutos disponibles, el grado de especialización funcional de aves se mantuvo relativamente estable. Además, el grado de especialización funcional se relacionó positivamente con la flexibilidad funcional (*i.e.*, la habilidad de las especies de aves para cambiar sus preferencias de consumo de frutos entre las diferentes estaciones). Estos resultados muestran que las especies de aves con mayor grado de especialización funcional fueron también las especies con una mayor flexibilidad para cambiar a tipos de recursos alternativos. Esta flexibilidad de las especies consumidoras puede ser un importante mecanismo para la estabilización de redes consumidor-recurso en respuesta al cambio climático u otros motores de cambio global.

En el segundo estudio se evaluó el carácter general del ajuste de rasgos en interacciones entre plantas de fruto carnoso y aves frugívoras. Para ello, combiné datos de rasgos morfológicos (para especies de plantas y aves) y datos de interacciones correspondientes a ocho redes de interacción entre plantas de fruto carnoso y aves frugívoras, muestreadas a lo

largo de la cordillera de los Andes tropicales y subtropicales. Los resultados mostraron que los rasgos de las especies relacionados con el ajuste por tamaño y los rasgos relacionados con el comportamiento de forrajeo de las aves fueron igual de importantes a la hora de determinar las interacciones entre las especies de plantas y aves en los Andes. Esto supone que el ajuste de rasgos morfológicos entre plantas de fruto carnoso y aves frugívoras es un fenómeno general en las redes planta-ave frugívora a lo largo de los Andes. Estos resultados son un primer paso hacia la deducción de reglas de interacción generales basadas en rasgos funcionales y proporcionan la base para predecir interacciones desconocidas a partir de rasgos funcionales en nuevas comunidades ecológicas que pueden resultar, por ejemplo, como consecuencia de la migración de especies y/o extinciones locales en respuesta al cambio climático.

Finalmente, el tercer estudio exploró los posibles cambios en la diversidad funcional de las comunidades de frugívoros al proyectar estas comunidades hacia un escenario futuro bajo condiciones de cambio climático. Para ello, combiné enfoques de biogeografía y ecología de comunidades y calculé la diversidad funcional de las comunidades de aves frugívoras actuales y futuras a lo largo de un gradiente altitudinal en los Andes tropicales. Los resultados indican que las comunidades a diferentes elevaciones a lo largo de una montaña tropical podrían verse afectadas de diferentes maneras. Concretamente, es probable que en un futuro las comunidades de tierras bajas se enfrenten a una pérdida de funcionalidad ecológica, mientras que las comunidades de altitudes medias se reorganicen, suponiendo una gran presión sobre estas comunidades para adaptarse a los cambios en su composición. Estos hallazgos sugieren que el cambio climático será un factor importante a la hora de estructurar las comunidades en el futuro.

En resumen, esta tesis contribuye a una comprensión general sobre cómo los rasgos funcionales de las especies definen el papel funcional que éstas cumple en una comunidad. Examino la flexibilidad de las especies para cambiar de recursos, la generalidad del mecanismo de ajuste de rasgos en las redes de interacciones y los cambios en la diversidad funcional de las comunidades bajo un escenario de cambio climático. A pesar de que esta tesis se centra específicamente en las interacciones mutualistas de dispersión de semillas en los trópicos, los conceptos y la teoría que analizo pueden ser aplicables en otros ámbitos, por ejemplo, en otras interacciones ecológicas como las redes de polinización. En conjunto, los resultados de esta tesis sugieren que es probable que la composición funcional de las comunidades cambie considerablemente en el futuro. Asimismo, identifico mecanismos que puedan ayudar a estabilizar a dichas comunidades. Por ejemplo, la flexibilidad funcional de las especies consumidoras podría ayudar a estas comunidades a reestructurarse y persistir en el futuro. La generalidad del ajuste de rasgos entre las especies interactuantes ayudía a identificar las reglas de interacción específicas que podrían aplicarse para predecir la potencial reorganización de las interacciones en futuras comunidades. Por lo tanto, esta tesis proporciona información valiosa sobre cómo mejorar las proyecciones de diversidad funcional y funcionamiento ecosistémico en condiciones futuras.



Chapter 1

General introduction

BIODIVERSITY AND ECOSYSTEM FUNCTIONING

Biodiversity is defined as the variability among all living organisms, at all levels of organization. This includes diversity within species, between species, and for whole ecosystems (UN 1992 Article 2, Tilman 1997). Levels of biodiversity increase from the poles to the tropics (Hillebrand 2004). The tropics contain exceptional concentrations of endemic species and host the majority of the world's biodiversity (Myers *et al.* 2000). Examples of taxa for which diversity peaks in the tropics include angiosperms (Jansson and Davies 2008) and birds (Hawkins *et al.* 2012). The tropical Andes in particular are known to be one of the most important global biodiversity hotspots (Myers *et al.* 2000). The Andes are the largest tropical mountain range in the world. Its broad latitudinal gradient, extended elevational gradient, and wet-dry gradient provide ideal conditions for its exceptional biodiversity (Herzog *et al.* 2011). This region is likely richer in biodiversity than any comparable area on Earth (Herzog *et al.* 2011) and it has the highest global share of endemic plants and vertebrates (Myers *et al.* 2000).

Biodiversity can be measured in different ways. Early biodiversity research focused mainly on species richness, thereby using the term as a synonym to the number of species that are present (Hooper *et al.* 2005, Reiss *et al.* 2009). The term biodiversity, however, equally covers the abundance of species, the evenness of species abundances, community composition, and differences in species functional traits and interactions (Hooper *et al.* 2005). There is a general consensus that biodiversity positively influences ecosystem functioning and its stability in space and time (Hooper *et al.* 2005). Ecosystem functions include ecosystem properties (materials, *e.g.*, carbon and organic matter; and rates of processes, *e.g.*, carbon cycle and plant net primary productivity), ecosystem goods (ecosystem products with a direct market value, *e.g.*, food, materials, medicines) and ecosystem services (ecosystem properties that benefit human endeavors, *e.g.*, cleaning water and air, crop pollination) (Hooper *et al.* 2005). Previously, research on the effect of biodiversity on ecosystem functioning has mainly focused on species richness, which tends to be positively related to ecosystem functioning (Hooper *et al.* 2005, Reiss *et al.* 2009). Many ecosystem functions are greatly influenced by species interactions between plants and animals, such as pollination and seed dispersal (*e.g.*, Jordano *et al.* 2007, Hoehn *et al.* 2008). The importance of species interactions has led to an increased interest in the relationship between interaction diversity and ecosystem functioning (Schleuning *et al.* 2015).

CLIMATE CHANGE

Climate change

Anthropogenic climate change is an increasingly important threat to biodiversity (Agard *et al.* 2012). Its direct and indirect effects have been reported on every continent, in every ocean, and in most taxonomic groups (Agard *et al.* 2012 and references therein). All research points to the conclusion that twentieth-century climate change has already severely affected biodiversity. Global climate has been changing at alarming rates, and global land surface temperatures have increased approximately 0.2 °C per decade since 1975 (Hansen *et al.* 2006). The current mean global temperature value lies within ~1 °C of the maximum temperature reached on Earth in the last million years. Some regions even exceed this warming rate, *e.g.*, temperatures in the tropical Andes have increased at a rate of approximately 0.32–0.34 °C per decade (Vuille and Bradley 2000). The International Panel on Climate Change (IPCC, 2001) presented future climate scenarios which suggested that the temperature along the Andean range will increase by about 3.2 °C over the next century, while precipitation will be reduced by ~20% (Christensen *et al.* 2007).

Two characteristics of the tropics might cause tropical species to be especially sensitive to climate change. First, species usually have narrow climatic tolerances, due to the low climatic variability and increased niche specialization in the tropics (Janzen 1967, McCain 2009). Second, species in the tropics are believed to occur near their temperature maximum (Khaliq *et al.* 2014) and tropical elevational temperature gradients are steep (5.2–6.5 °C per 1000 m elevation, Colwell *et al.* 2008). Consequently, species would be forced to move if the climate became even warmer. Finally, climate change acts in synergy with other drivers of global change, *e.g.*, habitat destruction and fragmentation (Brook *et al.* 2008). This is particularly relevant on tropical mountains, where climate change (Vuille and Bradley 2000) and land-use change (Sala *et al.* 2000) are affecting biodiversity simultaneously (Brook *et al.* 2008, Ferger *et al.* 2017). Therefore, climate change is expected to have an especially profound effect on biodiversity along the Andean range.

Species responses to climate change

In response to climate change, species are expected to shift their distributions poleward (Parmesan and Yohe 2003) and upward (Colwell *et al.* 2008) in order to follow their climatic niche. Latitudinal (poleward) shifts have been observed on all continents, in many different ecosystems and across a wide range of taxa (Parmesan 2006). Elevational (upwards) range shifts have received less attention, but have still been widely observed, *e.g.*, for butterflies (Parmesan 1996). While tropical regions remain understudied, examples of upward range shifts can still be found in a wide variety of taxa, including insects, vertebrates, and plants (*e.g.*, Pounds *et al.* 2005, Seimon *et al.* 2007, Chen *et al.* 2009, Feeley *et al.* 2011, Freeman and Class Freeman 2014).

Even though it has been shown that species are moving their ranges when subjected to climate change, it is not clear whether they will be able to move fast enough. Feeley *et al.* (2011) concluded that to respond to the temperature change in the tropical Andes (0.32–0.34 °C per decade, Vuille and Bradley 2000), a species would have to move 5.5–7.5 vertical meters per year. Their own analysis of tropical tree genera showed movement of 2.5–3.5 vertical meters upslope per year (Feeley *et al.* 2011), which is not fast enough to keep up with the predicted temperature increase. Explanations for why species might not be able to migrate fast enough to follow their climatic niches include limited dispersal ability (Corlett 2009), topographic obstacles (Dehling *et al.* 2014a, Rehm and Feeley 2016), and long generation times (Ibáñez *et al.* 2006, Lenoir *et al.* 2008). The inability of species to follow their climatic niches might result in large population losses or even local extinction of entire species (Feeley and Silman 2010a, Rehm and Feeley 2016).

Different species ranges will result in changes to the biodiversity of communities in mountainous areas (Parmesan 2006). Responses will vary between species with different traits (Keddy 1992) and the emigration and immigration of species can lead to a community turn-over along mountain ranges (Colwell *et al.* 2008). This turn-over in community composition will lead to changes in biotic interactions and ecosystem functioning. One way to study the response of species is to use a species distribution model (SDM). SDMs combine species occurrences with environmental variables to quantify current species-environment relationships, and can be used to project species across space and time (Guisan and Zimmerman 2000, Elith and Leathwick 2009). One application, therefore, could be to project communities into the future and asses the severity of changes in community composition under climate change (Thuiller 2004).

FUNCTIONAL DIVERSITY

Functional traits

Traits are defined as any feature measurable at the individual level, from a single cell to the whole organism. This implies that no information external to the organism (environmental or from other levels of organization) is necessary to define a trait (Violle *et al.* 2007). Traits include morphological (*e.g.*, beak size), physiological (*e.g.*, potential photosynthetic rate), phenological (*e.g.*, flowering time), and behavioral traits (*e.g.*, nocturnal vs. diurnal foraging) (Violle *et al.* 2007, Cadotte *et al.* 2011). It was originally proposed by Darwin (1859) that traits were to be mainly used as predictors of the performance of individual organisms. Recently, however, trait-based approaches have penetrated studies of higher organizational levels, like community and ecosystem ecology (*e.g.*, Lavorel and Garnier 2002, Petchey and Gaston 2002, Eviner and Chapin 2003, McGill *et al.* 2006). To be able to provide generality and predictability in community ecology, and to facilitate the synthesis with ecosystem ecology, traits should vary more between than within species (McGill *et al.* 2006).

For many research purposes, the most important type of traits are *functional traits*. These traits have an indirect impact on fitness via their effects on the three components of individual performance: growth, reproduction and survival (Reich *et al.* 2003, Violle *et al.* 2007). The functionality of communities and ecosystems is therefore a product of the functionality of all species that are present (Blüthgen and Klein 2011). Functional diversity, a quantification of trait diversity, can help understand complex natural systems through its systematic association with ecosystem functions (Petchey and Gaston 2006, Reiss *et al.* 2009).

Functional diversity

Recently, there has been an increased interest in the effects of species functional traits, and biotic interactions between species, on ecosystem functioning (Hooper *et al.* 2005, Schupp *et al.* 2010, Díaz *et al.* 2013, Valiente-Banuet *et al.* 2015). Functional diversity is a quantification of biodiversity which measures the values, and the ranges of values, of species traits that influence ecosystem functioning (Tilman 2001). Compared to traditional measures of biodiversity (like species richness) functional diversity presumes a more mechanistic link between species diversity and the ecological process studied (Cadotte *et al.* 2011). In other words, it aims to understand communities and ecosystems based on what organisms do in current communities, rather than on how many they are (Hooper *et al.* 2005, Flynn *et al.* 2009). To understand the link between diversity and ecosystem functioning, it is therefore important to first identify which traits relate to the ecosystem function studied (Violle *et al.* 2007), especially since this information is often incomplete (Tilman 2001).

Measuring functional diversity is complex, since species possess multiple traits at once and multiple species exist in an ecosystem together (Tilman 2001). Ordination methods provide the possibility to consider multiple traits, and multiple species at the same time (Mouillot *et al.* 2013). These ordinations lead to multidimensional trait spaces, in which one can place multiple species based on their respective functional trait values. There are a variety of complementary functional diversity metrics available, all of which measure different characteristics of species in the trait space (Mason *et al.* 2005, Villéger *et al.* 2008, Laliberté and Legendre 2010). Functional richness, for example, quantifies the proportion of overall functional space filled by a community (Villéger *et al.* 2008). Another aspect of functional diversity is the average dissimilarity between species in the functional trait space, largely independent of species richness. This dissimilarity indicates the potential for functional complementarity among species in a community, which can be measured with metrics like functional dispersion (Laliberté and Legendre 2010).

SPECIES INTERACTIONS

Mutualistic interaction networks

Ecosystems are composed of species that are bound together by biotic interactions. Species interactions between individuals, species, and trophic levels are considered to be the backbone of biodiversity, since they lay the architectural foundation of ecosystems (Bascompte and Jordano 2014, Jordano 2016a). Any kind of interaction is an essential element of an ecological community and will directly or indirectly affect ecosystem functioning (Thompson 1996, Chapin *et al.* 2000). Species interactions might be lost before a species is lost from an ecosystem (Säterberg *et al.* 2013, McConkey and O'Farrill 2016). One famous example of this loss of functionality is the "empty forest syndrome" (Redford 1992). A functionally empty forest is a forest where the biodiversity of plants and animals may appear intact, but species abundance is so diminished, *i.e.*, the number of biotic interactions in which species participate is so low, that species functional roles are lost. These functional losses may lead to the loss of essential ecosystem functions, such as pollination and seed dispersal, with substantial consequences for plant populations (Şekercioğlu 2011, Galetti *et al.* 2013). Therefore, it is of utmost importance to improve our knowledge of interaction rules and ecosystem functions derived by species interactions.

Mutualistic interactions are interactions of mutual benefit between species, *e.g.*, pollination and seed dispersal that benefits both plants and animals (Bascompte 2009). Animal-mediated seed dispersal is a crucial ecosystem function in tropical forests, where more than 90% of all woody plant species depend on animals to disperse their seeds (Howe and Smallwood 1982). Frugivorous birds are the most diverse and important seed dispersers in tropical forests (Herrera 2002, Kissling *et al.* 2009) and are essential for plant population dynamics. Frugivorous birds disperse seeds to sites distant from the mother tree, to previously unoccupied sites, and to distant sites with suitable environmental conditions (Howe and Smallwood 1982). This makes avian-mediated seed dispersal crucial for plant recruitment, gene flow among populations, and for range expansions of plant species (Howe and Smallwood 1982). The disruption of animal-mediated seed dispersal can lead to reduced seed removal rates and decreased seed dispersal distances (Markl *et al.* 2012), leading to modified spatial distributions of plant species (Rodríguez-Pérez *et al.* 2012).

Species interactions form intricate networks of species interdependence (Bascompte 2009), represented by species as nodes and biotic interactions as links between nodes (Bascompte and Jordano 2007). Mutualistic interactions are usually shown as bipartite networks; two groups of species with interactions between groups, but not within groups (Bascompte and Jordano 2007). Networks are characterized by a number of general properties or rules. For example, interaction networks are nested, *i.e.*, networks consist of some specialist species that interact with species that are a subset of the species with which generalists interact (Bascompte and Jordano 2007). Nestedness is thought to reduce the degree of competition and allows more species to coexist in a community (Bascompte *et al.* 2003, Bascompte and Jordano 2007). A nested network is asymmetrical, *i.e.*, specialist species interact only with generalist species, so if a plant species is highly dependent on an animal species, the animal is only weakly dependent on the plant (Bascompte *et al.* 2006). This asymmetry contributes to the persistence of specialist species, since specialists depend on the generalist species (Bascompte *et al.* 2003). Moreover, interaction networks have a modular pattern, *i.e.*, species within tightly connected subgroups are linked more to each other than to species in other subgroups. Modularity is supposed to increase community robustness and resistance to disturbance (Olesen *et al.* 2007). Finally, interaction networks are heterogeneous, *i.e.*, a few species are extraordinarily well connected, qualitatively and quantitatively, while the majority of species have few interactions (Jordano *et al.* 2003, Bascompte 2009).

The concept of the Eltonian niche (Elton 1927, Chase and Leibold 2003) suggests that species that interact with different sets of interaction partners fulfill different functional roles in ecological communities. In addition, the distribution and magnitude (interaction strength) of the links in a network provide insight into the functional role that each species fulfills (Blüthgen *et al.* 2006). It can therefore be derived that matching traits can define the functional role that a species fulfills in an interaction network (Schleuning *et al.* 2015). One way to measure the role of individual species in interaction networks is the degree of specialization on specific interaction partners (Waser and Ollerton 2006, Olesen *et al.* 2011a, Brodie *et al.* 2014). Functionally speaking, species that interact with functional traits of partners that no, or only few, other species interact with are functionally specialized (Bellwood *et al.* 2006, Dehling *et al.* 2016). Functional specialists may be disproportionally important to ecosystem functioning as they contribute ecological functions that few other species can provide (Mello *et al.* 2015).

Trait matching

The formation of interactions between two species in a network depends on the compatibility of their functional traits (Jordano 1987, Stang *et al.* 2009). There is a large body of literature on the importance of trait matching in mutualistic interaction networks (*e.g.*, Wheelwright 1985, Woodward and Warren 2007, Stang *et al.* 2009, Eklöf *et al.* 2013, Dehling *et al.* 2014b, Maglianesi *et al.* 2015). The comparison of functional trait diversity between communities (based on matching traits of interacting species) might also be better suited than correlations of species numbers to reveal the mechanisms behind large-scale diversity patterns of interacting species (Dehling *et al.* 2014b). There are two pathways that might lead to trait matching in interaction networks. First, it could be the result of coevolution, *i.e.*, interacting species imposed selection pressure on each other, which led to a reciprocal adaptation of functional traits to their specific interaction partners (*e.g.*, Janzen 1980, Jordano *et al.* 2003, Bascompte *et al.* 2006). Alternatively, trait matching could be the result of ecological fitting, *i.e.*, species evolved their traits independently, but they interact because they co-occur and their traits are closely matched (Janzen 1985, Agosta 2006).

There are different types of matching traits. Size matching corresponds to the functional relationship between consumer and resource sizes, *e.g.*, flower size is related to proboscis and bill size in pollination networks (Stang *et al.* 2009, Maglianesi *et al.* 2015). The matching of size related traits has been well studied, as it can form an important constraint in the formation of interactions (Moermond and Denslow 1985, Wheelwright 1985, Levey 1987). For example, bill size restricts the maximum size of a fruit that a bird can handle and/or swallow in seed dispersal networks (Wheelwright 1985, Stang *et al.* 2009, Garibaldi *et al.* 2015). Another type of trait matching relates to the foraging behavior of consumer species, which influences whether resources are encountered by, and attractive to, the consumer. For example, the theory of optimal foraging proposes that large species require energy-rich resources (Belovsky 1997, Petchey *et al.* 2008). Therefore, animals with a large body size tend to prefer energy-rich resources (Krebs and Davies 1993), *e.g.*, large frugivores, such as monkeys, feed exclusively on fruits with large crops (Flörchinger *et al.* 2010). Another important foraging trait is animal mobility. Animal mobility directly influences which resources are encountered and accessible for animals. For instance, in forests with multiple strata the wing shape of birds and bats determines in which forest stratum these animals forage (Moermond and Denslow 1985, Norberg and Rayner 1987, Schaefer *et al.* 2002, Swartz *et al.* 2003, Schleuning *et al.* 2011).

OBJECTIVES OF THE THESIS

The overall objective of this thesis is to contribute to a better understanding of functional diversity in seed dispersal networks. It focuses on mutualistic interactions between frugivorous birds and fleshy fruited plants in the Andes, a global biodiversity hotspot for both of these groups (Kissling *et al.* 2009, Jansson and Davies 2008). Specifically, this thesis takes a trait-based approach to studying the functional specialization of frugivorous birds from three different perspectives (chapters 2–4). First, I focus on the seasonal variation of interactions between birds and plants (Fig. 1.1, Q1 "*seasonal variation*"). Second, I focus on the spatial variation of trait matching in seed dispersal networks (Fig. 1.1, Q2 "*spatial variation*"). Finally, I use future projections to provide insights into the potential future functional composition of frugivore communities (Fig. 1.1, Q3 "*future projections*"). The structure of the thesis is summarized in Fig. 1.1 and the specific objectives of the three studies are outlined below.

Q1. How flexible do frugivorous bird species respond to seasonal fluctuations in plant traits?

It has long been known that plant phenology leads to seasonal fluctuations in resource availability, also in the tropics (Schaefer *et al.* 2002), but how consumer species respond to these temporal fluctuations has received little attention. In chapter 2, I aim to answer this question by testing how flexible frugivorous bird species are to respond to seasonal fluctuations in plant traits (Fig. 1.1, Q1). To this end, I used a trait-based analysis where I placed each bird in the plant trait space, based on their feeding preference. Comparing trait space locations of a species in different seasons can indicate how much a bird species moves between functionally distinct plant species over time.

First, I test the hypothesis that the degree of functional specialization stays constant throughout the year. If species tend to maintain a similar degree of functional specialization across seasons, this would indicate that they always tend to fulfill a similar functional role in the network, *i.e.*, they would maintain their role as the disperser of specific plant species. Second, to explore the flexibility with which species are able to shift between different resource types, I test the relationship between functional specialization and functional flexibility. A bird species that feeds on functionally distinct plant species in different seasons would have a higher functional flexibility than a species which always feeds on fruits with similar traits. In the absence of their preferred fruit type, species might need to switch to alternative fruits in certain seasons. Functionally specialized species, however, might be dependent on specific interaction partners (Brodie *et al.* 2014), which could make them less flexible to respond to spatial or temporal fluctuations (Fang and Huang 2012).

Q2. How general is trait matching in interactions between plants and frugivorous birds?

Since many studies have highlighted the importance of trait matching in mutualistic networks (*e.g.*, Wheelwright 1985, Woodward and Warren 2007, Stang *et al.* 2009, Eklöf *et al.* 2013, Dehling *et al.* 2014b, Maglianesi *et al.* 2015), it might be possible to identify general interaction rules. Such general rules could make it possible to project which species pairs are likely to interact in new and future communities (Morales-Castilla *et al.* 2015, Bartomeus *et al.* 2016). The first step in the development of such rules would be to test how general trait matching, between fleshy fruited plants and frugivorous birds, is in interaction networks. In chapter 3, I explore the generality of trait matching by combining the data from eight mutualistic seed dispersal networks collected in five countries along a large geographical gradient, covering the tropical and subtropical Andean range (Fig. 1.1, Q2).

I hypothesize that trait matching is a general mechanism in interaction networks. I approach this hypothesis from two angles. First, I test which trait pairs (size matching and foraging related) are important in shaping plant-animal interactions. I expect that size matching related traits are more important for the matching between plants and birds than foraging related traits, since size matching imposes a direct constraint on the likelihood of interactions (Wheelwright 1985, Sebastián-González *et al.* 2017). Second, since both trait matching and the degree of functional specialization are determined by the same morphological traits, I test which functional traits are related to the functional role of a species in a network. Large-fruited plants and larger-billed birds are expected to be among the most functionally specialized species in these communities. These species are reciprocally specialized on each other (Moermond and Denslow 1985, Wheelwright 1985) and are relatively rare in the respective communities (Wheelwright 1988).

Q3. How does climate change affect trait diversity of frugivorous bird communities?

Climate change forces species to move to higher elevations to track their climatic niche (Colwell *et al.* 2008). These changes to species ranges will lead to changes in the biodiversity of communities in mountainous areas (Parmesan 2006). However, little is known about how the functional diversity of communities along mountain ranges may change. In chapter 4 I explore the potential future changes in functional diversity of avian frugivore communities under climate change (Fig. 1.1, Q3). Specifically, I focus on the diversity of the functional traits relevant to the ecosystem function of bird-mediated seed dispersal. This study combines approaches from biogeography (species distribution models; SDMs) with community ecology (functional diversity; FD) to project bird communities into the future.

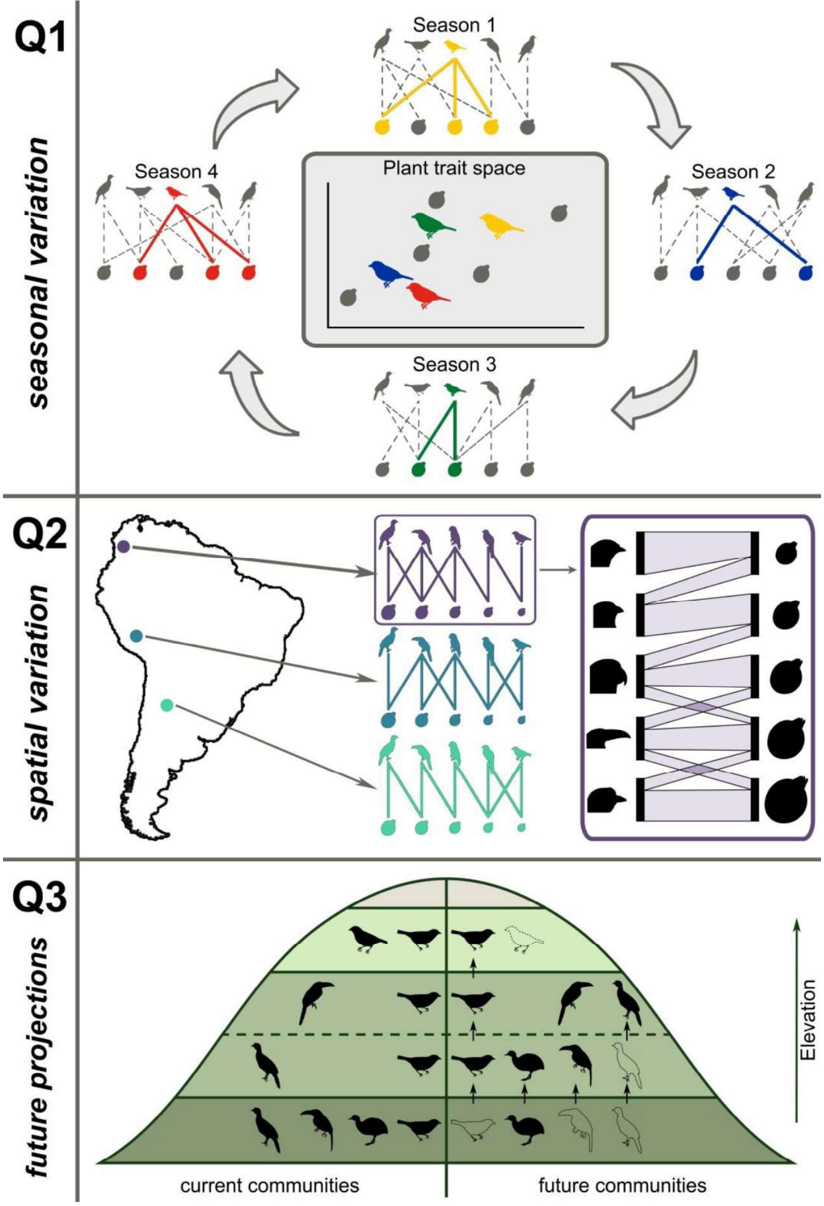
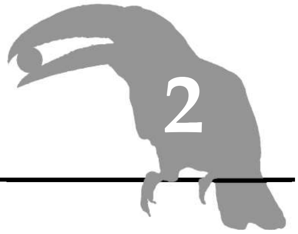


Figure 1.1. Conceptual figure illustrating the three main questions explored in this thesis. (Q1) *Seasonal variation in interactions*. In seasonal networks between frugivorous birds and fleshy-fruited plants, the interaction links between birds and plants vary over time. The thick lines show how changes in the plant community lead to changing interactions for one particular bird species. Exploring how the fruit preference of a bird species in plant trait space changes across seasons can help to assess how flexible frugivorous bird species respond to fluctuations in plant traits. (Q2) *Spatial variation in trait matching*. Trait matching assumes that a higher compatibility between functional traits of birds and plants will lead to higher interaction frequencies. Comparing the degree of trait matching in various plant-bird interaction networks from across the Andes can therefore help to assess the generality of trait matching in interaction networks between fleshy fruited plants and frugivorous birds. (Q3) *Future projections of functional diversity*. Climate change will lead to changes in the functional composition of frugivore communities, *e.g.*, via shifts in species ranges (outlines; species moved out of the respective elevational level) or species extinctions (dotted outline; species disappear from entire gradient). Comparing current and projected future communities can help to answer the question how climate change might affect the trait diversity of frugivorous bird communities.

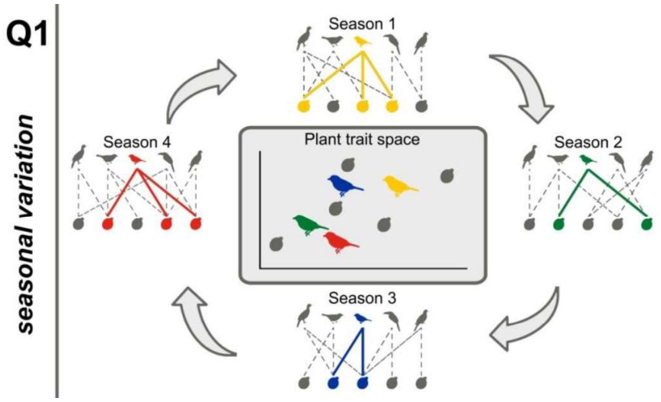
I hypothesize that communities at different elevations might respond differently to climate change. Upward moving bird species from the lowest elevations might lead to a net loss of species from the lowlands, since there are no lower elevations from where new species could move in (Fig. 1.1, Q3, lowest elevational level). This process is referred to as "biotic attrition" (Colwell *et al.* 2008, Feeley and Silman 2010b). At the mid-elevations species would be forced to move upwards as well, but here they could be replaced by species immigrating from the lowlands. This functional compensation from the lowlands is expected to lead to a functional turnover at these elevational levels (Fig. 1.1, Q3, mid-elevational levels). At the highest elevations, species might be lost since frugivorous bird species are not able to move past the current treeline (Rehm and Feeley 2016), leading to a decrease in functional diversity (Fig. 1.1, Q3, highest levels). At a community level, however, it remains unclear to what extent this loss can be functionally compensated for by immigration of species from mid-elevations.

The topics discussed in this thesis contribute to a better understanding of the role of functional traits in structuring species interactions. I explore how communities interact and function under current conditions and how the functionality of these communities might change under projected future conditions, by studying the functional dynamics of the interactions across space and time. The results of this thesis contribute to the overall aim to improve the predictability of the diversity, interactions, and function of these networks in the future.



Chapter 2

Functionally specialized birds respond flexibly to seasonal changes in fruit availability



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FUNCTIONALLY SPECIALIZED BIRDS RESPOND FLEXIBLY TO SEASONAL CHANGES IN FRUIT AVAILABILITY

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SUMMARY

1. Interactions between resource and consumer species result in complex ecological networks. The overall structure of these networks is often stable in space and time, but little is known about the temporal stability of the functional roles of consumer species in these networks.

2. We used a trait-based approach to investigate whether consumers (frugivorous birds) show similar degrees of functional specialization on resources (plants) in ecological networks across seasons. We additionally tested whether closely related bird species have similar degrees of functional specialization and whether birds that are functionally specialized on specific resource types within a season are flexible in switching to other resource types in other seasons.

3. We analyzed four seasonal replicates of two species-rich plant–frugivore networks from the tropical Andes. To quantify fruit preferences of frugivorous birds, we projected their interactions with plants into a multidimensional plant trait space. To measure functional specialization of birds, we calculated a species' functional niche breadth (the extent of seasonal plant trait space utilized by a particular bird) and functional originality (the extent to which a bird species' fruit preference functionally differs from those of other species in a seasonal network). We additionally calculated functional flexibility, *i.e.*, the ability of bird species to change their fruit preference across seasons in response to variation in plant resources.

4. Functional specialization of bird species varied more among species than across seasons, and phylogenetically similar bird species showed similar degrees of functional niche breadth (phylogenetic signal $\lambda = 0.81$) and functional originality ($\lambda = 0.89$). Additionally, we found that birds with high functional flexibility across seasons had narrow functional niche breadth and high functional originality per season, suggesting that birds that are seasonally specialized on particular resources are most flexible in switching to other fruit resources across seasons.

5. The high flexibility of functionally specialized bird species to switch seasonally to other resources challenges the view that consumer species rely on functionally similar resources throughout the year. This flexibility of consumer species may be an important, but widely neglected mechanism that could potentially stabilize consumer–resource networks in response to human disturbance and environmental change.

INTRODUCTION

Both mutualistic interactions (*e.g.*, between plants and pollinators) and antagonistic interactions (*e.g.*, between parasites and their hosts) are organized in ecological networks (Ings *et al.* 2009) that describe the interactions between species in ecological communities (Bascompte 2009). The general structure of these networks has been widely studied (*e.g.*, Petanidou *et al.* 2008, Dáttilo *et al.* 2013, Plein *et al.* 2013). However, less is known about the functional roles of individual species within these networks, *e.g.*, about their importance for ecosystem functions such as pollination or seed dispersal. Previous studies have shown that species' traits and phylogenetic history influence the functional roles of species in ecological networks (Rezende *et al.* 2007, Schleuning *et al.* 2014, Dehling *et al.* 2016, Lavabre *et al.* 2016), but the spatial and temporal variability of these roles remains less explored (Burkle and Alarcón 2011, Mello *et al.* 2013, Trøjelsgaard *et al.* 2015, among others).

One way to measure the role of individual species in ecological networks is the degree of specialization on specific interaction partners (Brodie *et al.* 2014). There are different, complementary ways to measure species' specialization. For instance, specialization of species in interaction networks can be quantified by the number of interaction partners (*e.g.*, Alarcón *et al.* 2008, Olesen *et al.* 2011a). While this simple measure of species' niche breadth does not account for trait similarity among resource species, the concept can be expanded to a measure of the functional niche breadth of consumers by accounting for trait differences among resource species (Fig. 2.1). Specialization can also be measured in a community context where a specialist species is defined as a species that interacts with a distinct set of species in the network (Blüthgen *et al.* 2008, Ruggera *et al.* 2016). According to this concept, functionally specialized species interact with functional characteristics of partners that no or only few other species interact with (Bellwood *et al.* 2006, Dehling *et al.* 2016). Such species have a high degree of functional originality in the community. As morphological and functional specialization of species are closely linked (Dehling *et al.* 2016) and many morphological traits are phylogenetically conserved (Webb *et al.* 2002, Dehling *et al.* 2014a), phylogenetically related species might be expected to exhibit similar degrees of functional specialization, both in terms of their functional niche breadth and their functional originality.

Interactions between species vary in space and time (*e.g.*, Petanidou *et al.* 2008, Benadi *et al.* 2013), but emerging network properties are often surprisingly stable (*e.g.*, Petanidou *et al.* 2008, Dáttilo *et al.* 2013, Plein *et al.* 2013, but see Olesen *et al.* 2010). What remains less clear is to what extent the functional roles of species within ecological networks vary across space and time. For instance, plant phenology leads to fluctuations in resource availability throughout the year, and consumer species have to respond to these fluctuations, *e.g.*, by shifting to other resource types or between different species of the same resource type (Carnicer *et al.* 2009, Kissling *et al.* 2009). Thus far, the flexibility by which species respond to seasonal changes in the availability of resources has been little studied in the context of species interaction networks. A trait-based approach allows to assess the functional flexibility of a species by quantifying the trait dissimilarity between species' interaction

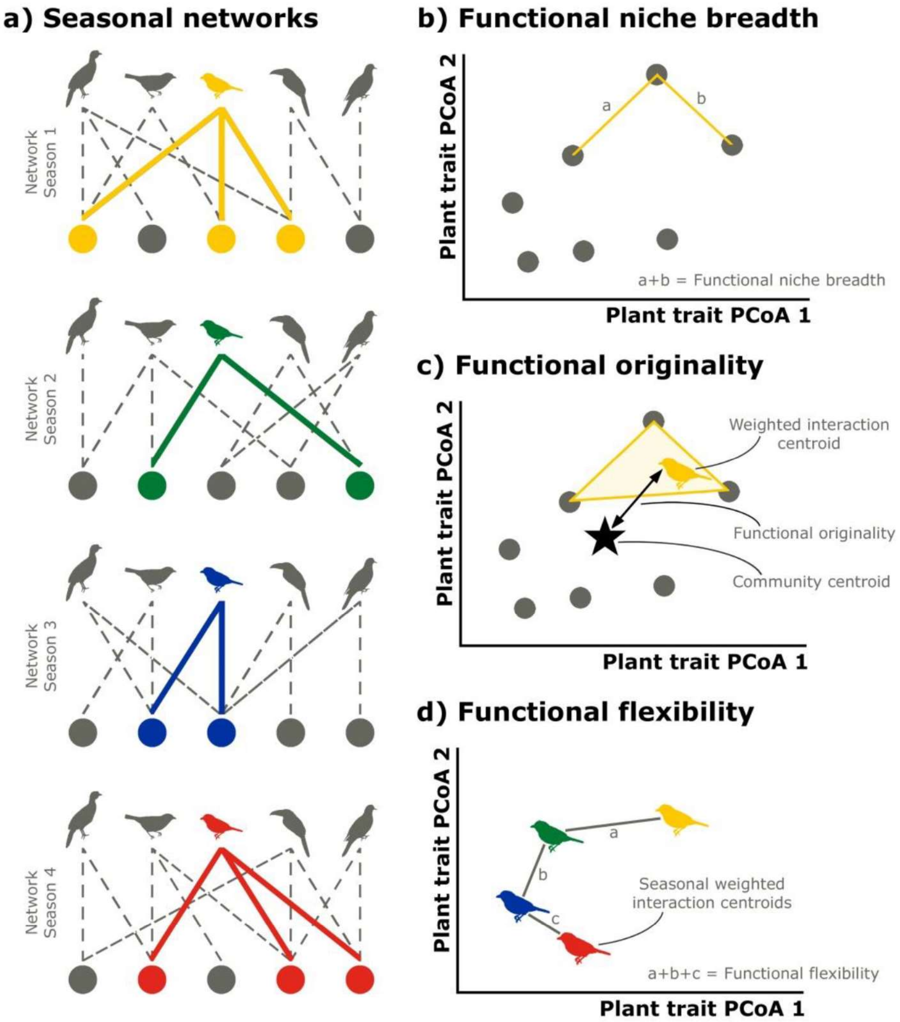

Figure 2.1. Seasonal variation in interaction networks and derived measures of functional niche breadth, functional originality and flexibility. (a) In seasonal networks of frugivorous birds and fleshy-fruited plants, the interactions (*i.e.*, links) between birds and plants vary over time. Here, all bird species are present in each seasonal network, but the availability of plant species with certain traits (*e.g.*, in terms of fruit size, crop mass, etc.) changes between seasons. The thick lines show how changes in the use of plant species lead to changing interactions for one particular bird species. (b) Functional niche breadth measures the range of trait values of plants on which a bird species feeds. It is calculated as the length along a minimum spanning tree between all plant species that a bird feeds on in a particular season. (c) Functional originality (*i.e.*, the extent to which bird species interact with plant partners that only few other species interact with) measures a bird's fruit preference within the plant functional trait space in a given season (*i.e.*, its interaction centroid) relative to the seasonal community average (*i.e.*, the community centroid). The interaction centroid of a bird species equals the weighted average of principal coordinates of all plant species interacting with the respective bird species. The community centroid is the mean of the interaction centroids of all bird species in the community. Functional originality is the Euclidean distance between the bird species' interaction centroid and the community centroid. (d) Functional flexibility measures the change in fruit preference of a bird species in plant trait space across seasons. It is calculated as the length along a minimum spanning tree between the four seasonal interaction centroids of each species.

partners in space or time. Species that switch between interaction partners with distinct traits will have a higher functional flexibility than species that are restricted to species with similar traits.

An open question is to what extent functional specialization and functional flexibility of species are related to each other in species interaction networks. Species that are functionally specialized in a given season (*i.e.*, species that have a low functional niche breadth or a high functional originality) might need to switch to alternative resources in other seasons, and hence be seasonally flexible in their resource choice. Furthermore, species that are less specialized in their resource choice are probably switching less often to other resource types. However, an alternative prediction might be that functionally specialized species are dependent on specific interaction partners (Brodie *et al.* 2014), and therefore show less flexibility in response to spatial or temporal resource fluctuation (Fang and Huang 2012). This could mean that networks with many specialized species might be unstable due to a high risk of secondary species extinction in response to the loss of interaction partners (Colwell *et al.* 2012, Säterberg *et al.* 2013, Brodie *et al.* 2014). Hence, it is important to investigate to what extent species that are functionally specialized in a given season are able to switch to alternative resources in other seasons. This analysis provides a first test on how flexible consumer species may also be more flexible in response to other types of resource fluctuations, *e.g.*, as a result of human impacts.

In the tropics, many plant and animal species form mutualistic seed dispersal networks (Schleuning *et al.* 2012). Thus far, little is known about how animal species in these networks respond to seasonal changes in fruit availability. Here, we quantify seasonal changes in plant functional trait space (related to fruit size, plant height and crop mass) of two plant–frugivore networks sampled in the Andes of south-east Peru and apply a trait-based analysis to test whether seasonal variation in fruit resources affects the functional specialization of obligate avian fruit consumers. We then test, controlling for the phylogenetic relatedness among species, whether the flexibility of birds regarding their fruit choice across seasons is related to the degree of seasonal specialization on particular fruit types. We measure this functional specialization in two ways: as species' functional niche breadth in a given season and as functional originality compared to other species in seasonal seed dispersal networks. Our general aim was to examine the temporal variation of functional specialization of avian consumers in these plant–frugivore networks within and across seasons. Specifically, we ask: (i) To what extent does functional specialization of bird species vary across species and seasons? (ii) Are phylogenetically related species similarly specialized in their functional resource use? (iii) Is there a relationship between the degree of functional specialization within seasons and functional flexibility across seasons? We expect (i) more variation in functional specialization across species than across seasons and (ii) a phylogenetic signal in both measures of functional specialization. We did not have a clear expectation about (iii) the relationship between functional specialization per season and functional flexibility across seasons as both a positive and a negative relationship could be expected.

MATERIALS AND METHODS

Interaction networks and functional traits

We collected interaction networks of frugivorous birds and fleshy- fruited plants at two sites in the Kosñipata valley in the Manú Biosphere Reserve in the Andes of south-east Peru (Dehling *et al.* 2014b), a global hotspot of avian frugivore diversity (Kissling *et al.* 2009). One network, 'San Pedro', was located at 1500 m a.s.l. (hereafter 'm') in lower montane forest. The other, 'Wayqecha', was located at 3000 m in upper montane forest.

At each location, data were collected during four time periods (below referred to as 'seasons'). Sampling was done approximately every 3 months between December 2009 and September 2010, resulting in four seasonal replicates of each network (Dehling *et al.* 2014b). The first two seasons cover the beginning and peak of the rainy season, the third and fourth season the beginning and peak of the dry season. We installed 100 m × 30 m plots (eight plots in San Pedro, six plots in Wayqecha) and visually recorded seed removal by frugivorous birds on all fleshy-fruited plant species located in these plots. Only true seed removal events were included, *i.e.*, fruit swallowing or carrying fruits away. During each season, every plot was observed on five consecutive days between dawn and noon for a total of 30 h. The total observation time was 720 h in Wayqecha and 960 h in San Pedro, resulting in well-sampled interaction networks at both locations (Dehling *et al.* 2014b, Fig. S2.1).

We sampled four morphological plant traits that are of key importance for plant–frugivore interactions (Dehling *et al.* 2014b): fruit length, fruit diameter, plant height and crop mass. Traits were measured from plant individuals in the field. Fruit length, fruit diameter and fresh fruit mass were measured on at least 20 fruits per species collected from one to three individuals. Plant height and number of fruits were measured on all individuals of a species present in a plot. Plant height was measured as the maximum height of an individual using a range finder. For epiphytes, we recorded the height at which they grew. Number of fruits was counted per plant individual. When many fruits were present, fruits were counted for a part of the plant and then the total number of fruits was extrapolated to the entire plant individual. When infructescences contained many fruits, we counted the number of fruits per infructescence, the number of infructescences per individual and then estimated the total number of fruits. Crop mass was calculated as the product of the mean number of fruits per plant and the mean fruit mass. We log-transformed fruit length, fruit diameter and crop mass prior to further analysis to approximate a normal distribution. For all traits, we used the species mean across individuals in the analysis.

Seasonal variability in plant trait spaces

We followed Villéger *et al.* (2008) and used a principle coordinate analysis (PCoA) to project plant species into a multidimensional trait space. We used Mahalanobis distances between species as recommended for morphological species' traits (Botta-Dukát 2005) and projected all plant species (for all seasons and both sites) into a single four-dimensional PCoA space

(Dehling *et al.* 2016). The four, resulting orthogonal principal coordinates represent the total variation in the four plant traits and describe the morphological differences among species by species-specific coordinates along the respective axes (see Fig. S2.2 for the correlations of the original traits on the respective axes). For each seasonal network, the principal coordinates of the plant species fruiting in the respective season were extracted to analyses the seasonal variability in plant trait space. For each of the four seasonal networks at both sites (San Pedro and Wayqecha), we calculated two metrics of functional diversity from the PCoA trait space to quantify seasonal changes in plant trait diversity: functional richness (FRic) and functional dispersion (FDis). Functional richness measures the entire volume of niche space filled by species in the community (Mason *et al.* 2005) and is independent of species' frequencies. In contrast, functional dispersion quantifies the weighted average distance to the weighted centroid of a community (Laliberté and Legendre 2010). Here, weighting was done with the total number of avian visits to each plant species in the respective network.

Functional niche breadth

We restricted all species-level analysis to bird species which are dependent on fruits year-round, *i.e.*, frugivorous birds that were present in all four seasons in either one or both networks (n = 33 species; 20 species in San Pedro, 11 species in Wayqecha and 2 additional species in both networks). For these species, we calculated functional niche breadth per season, *i.e.*, the minimal distance needed to connect all interaction partners of a bird species in plant trait space within a seasonal network. For each seasonal network and bird species, we extracted PCoA coordinates of all plant species that a bird species interacted with and calculated the minimum Euclidian distance needed to connect these species (minimum spanning tree, Fig. 2.1b). We used this approach instead of a functional volume because distances can be computed even for species with few interaction partners. Species recorded to interact with only a single plant partner were assigned a minimum functional niche breadth, defined by half of the minimum distance that was recorded across all species with more than one partner. Functional niche breadth therefore indicates to what extent a bird species utilized the available plant trait space in a given season, independent of the frequencies of interactions with the respective plant partners. Functional niche breadth is an inverse measure of functional specialization and is largest for generalists, *i.e.*, species that interact with many functionally different plants. Accordingly, the metric is strongly correlated with other specialization measures such as the standardized degree of a species, *i.e.*, the proportion of utilized plant species relative to all available plant species in a given season (r = 0.95, $P < 0.01$, n = 33 species). However, it was not related to network specialization measures such as *d'* (Blüthgen *et al.* 2008) which account for the community context ($r = -0.08$, $P = 0.51$, $n = 33$ species).

Functional originality

We calculated functional originality (following the analytical framework of Dehling *et al.* 2016) as a second measure of functional specialization per season because it accounts for the community context (Fig. 2.1c). For each seasonal network, we selected all plant species that a specific bird species fed on. The principal coordinates of these plant species were then weighted by interaction strength and averaged to derive the weighted seasonal interaction centroid for each bird species (Fig. 2.1c). Interaction strength was quantified as the ratio between the respective interaction frequency (total number of bird visits to a specific plant species) and the total number of interaction events of the respective bird species across all plant species (Bascompte and Jordano 2007). We then measured functional originality for each bird species by calculating the Euclidian distance between the weighted seasonal interaction centroid of the respective bird species and the seasonal community centroid (Fig. 2.1c, Dehling *et al.* 2016). The community centroid was calculated as the unweighted mean of all bird species' interaction centroids in each seasonal network. Thus, functional originality measures functional specialization of a bird species in a given season relative to that of other species in the community (Bellwood *et al.* 2006). Functional originality was moderately correlated with functional niche breadth ($r = -0.43$, $P < 0.01$, $n = 33$ species) and with network specialization measures such as standardized degree ($r = -0.48$, $P < 0.01$, $n = 33$ species) and d' ($r = 0.49$, $P < 0.01$, $n = 33$ species).

Seasonal variation in functional niche breadth and functional originality

We tested whether functional specialization (*i.e.*, functional niche breadth and functional originality calculated for each seasonal network) of bird species showed seasonal variation. We fitted linear mixed-effect models ('lme4' package in R) with either functional niche breadth or functional originality as response variable, species identity and season as fixed effects, and network identity as random effect. Functional niche breadth and functional originality were log-transformed to approximate normality of model residuals. We further scaled functional niche breadth and functional originality to a mean of 0 and standard deviation of 1 within each seasonal network. This ensured that differences in the available plant trait space between seasons did not bias the degree of functional specialization of species when comparing different seasonal networks. We tested the significance of the fixed-effect terms with a type II ANOVA ('car' package in R) using the chi-square (χ^2) test statistic. This approach allows testing the fixed effects independent of the sequence of the terms in the model. In addition, we calculated the partial R^2 for season and species identity by computing the proportion of variance explained by the respective factor relative to the variance explained by other fixed and random factors plus the residual variance (Nakagawa and Schielzeth 2013). The partial R^2 values indicate how much of the variation in functional niche breadth and functional originality can be explained by the different factors. If species identity has a higher partial R^2 than seasons, species have similar functional specialization throughout the year, despite of seasonal variation.

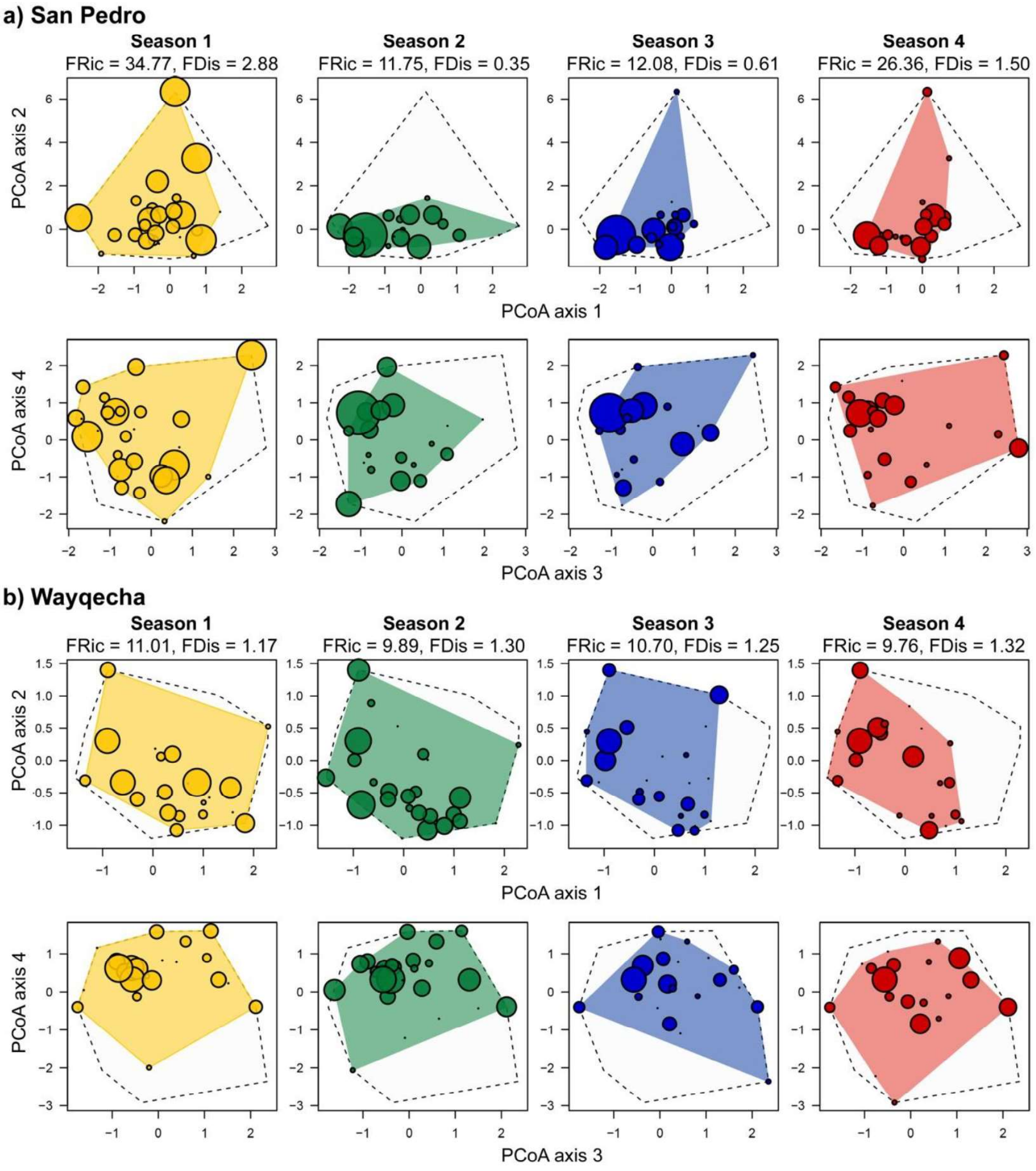

Figure 2.2. Seasonal trait spaces of fleshy-fruited plants at (a) San Pedro (1500 m a.s.l.) and (b) Wayqecha (3000 m a.s.l., both Manú Biosphere Reserve, Peru). Seasons 1 and 2 cover the rainy season, and seasons 3 and 4 cover the dry season. The principal coordinate analysis is based on fruit length, fruit diameter, plant height and crop mass of all plants in the two networks. The black stippled polygon illustrates the functional trait space of the fleshy-fruited plants in the respective network over the entire year, the colored overlay the functional trait space available in the respective season. Each dot represents one plant species; dot size corresponds to the log-transformed number of interaction events of the respective plant species with all frugivorous birds in the respective network. Functional richness (FRic) and functional dispersion (FDis) values of each seasonal trait space are shown above each panel for the respective season.

Phylogenetic signal of functional niche breadth and functional originality

We expected that phylogenetically closely related bird species show similar degrees of functional specialization. For this, we tested the phylogenetic signal in functional niche breadth and functional originality (with log-transformed and scaled mean values across the four seasons for each bird species) by estimating the lambda statistic (Pagel 1999). We constructed a phylogenetic tree of all included bird species (n = 33 species) using a global bird phylogeny (Jetz *et al.* 2012). A set of 10,000 trees was downloaded from birdtree.org using the 'Hackett All Species' backbone. We used TreeAnnotator v1.8.1 (BEAST v 1.8.1, Drummond *et al.* 2012) to combine these trees into one consensus tree (using the 'maximum clade credibility tree' option with median node heights). Statistical significance of the phylogenetic signal was tested using a likelihood ratio test (comparing the phylogenetic signal to a lambda of zero).

Functional flexibility

We defined functional flexibility of all bird species as their ability to switch seasonally between plant species with different traits. Functional flexibility was quantified as the minimum Euclidian distance connecting the four seasonal interaction centroids of a given bird species in a minimum spanning tree (Fig. 2.1d). The distances indicate how much a bird changes its fruit preference throughout the year, with a high functional flexibility value indicating that a bird feeds on different plant traits in different seasons. Functional flexibility was log-transformed to approximate normality of model residuals.

Relationship between functional specialization and flexibility

To test the relationship between functional specialization within seasons and functional flexibility across seasons, we fitted two linear phylogenetic generalized least-squares models (PGLS, *i.e.*, linear regression models controlling for phylogenetic relatedness among species) with functional flexibility as response variable and functional niche breadth and functional originality as predictors respectively. For this analysis, the seasonal values of functional niche breadth and functional originality were averaged for eac h species across networks. There was no need to account for site-specific differences among species because the relationship between functional flexibility and functional specialization showed qualitatively similar patterns for the networks sampled at San Pedro and Wayqecha. In the PGLS, a maximum likelihood approach was used to optimize Pagel's lambda branch length transformation (Freckleton *et al.* 2002).

To test whether the observed relationship between functional flexibility and the two measures of functional specialization was stronger than expected at random, we implemented two null models. The first null model used the Patefield algorithm (Patefield 1981), while the second null model used the method proposed by Vázquez *et al.* (2007). These null models randomized the observed interaction events, but maintained the total interaction frequency per species (Patefield 1981) or the connectance of the network (Vázquez *et al.* 2007). The connectance of the network is the proportion of realized links relative to all possible links in the network (Vázquez *et al.* 2007). Each seasonal network was randomized 100 times, according to the respective null model. We calculated functional niche breadth and functional originality of each bird species in each randomized seasonal network in the

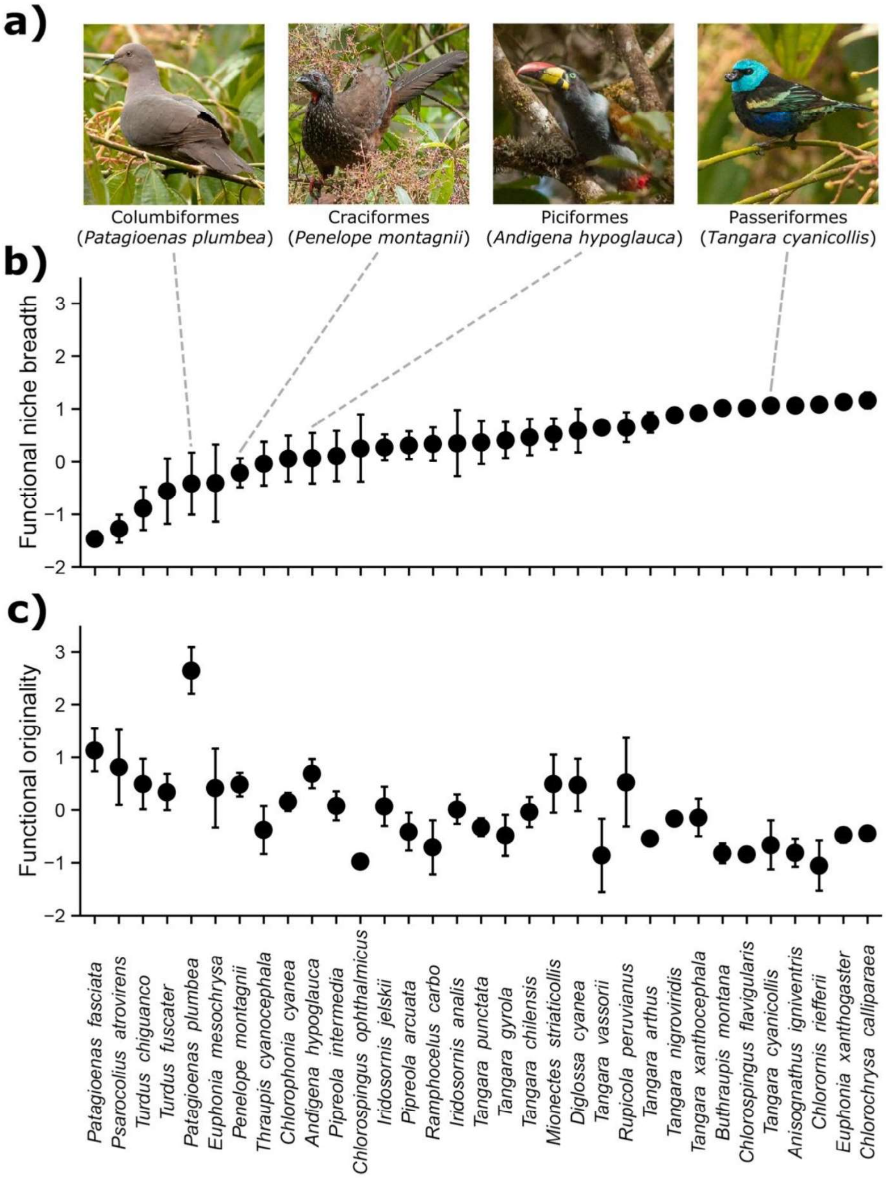

Figure 2.3. Functional niche breadth and functional originality of frugivorous birds (n = 33 species). (a) Examples of bird species from the four bird orders that are present in the studied plant–frugivore networks: Columbiformes (*Patagioenas plumbea*), Craciformes (*Penelope montagnii*), Piciformes (*Andigena hypoglauca*) and Passeriformes (*Tangara cyanicollis*). (b) Functional niche breadth and (c) functional originality for each bird species. The values in (b, c) represent mean and standard error (SE) of the respective seasonal values. Photo credit: D.M. Dehling.

same way as in the observed network and also computed the functional flexibility of species across the randomized seasonal networks. For each null model run, we applied a PGLS to test the relationship between functional niche breadth and flexibility and between functional originality and flexibility respectively. We extracted the 2.5% and 97.5% quantiles of the modelled slopes from the 100 null model runs and then compared their 95% confidence interval to the respective observed relationship.

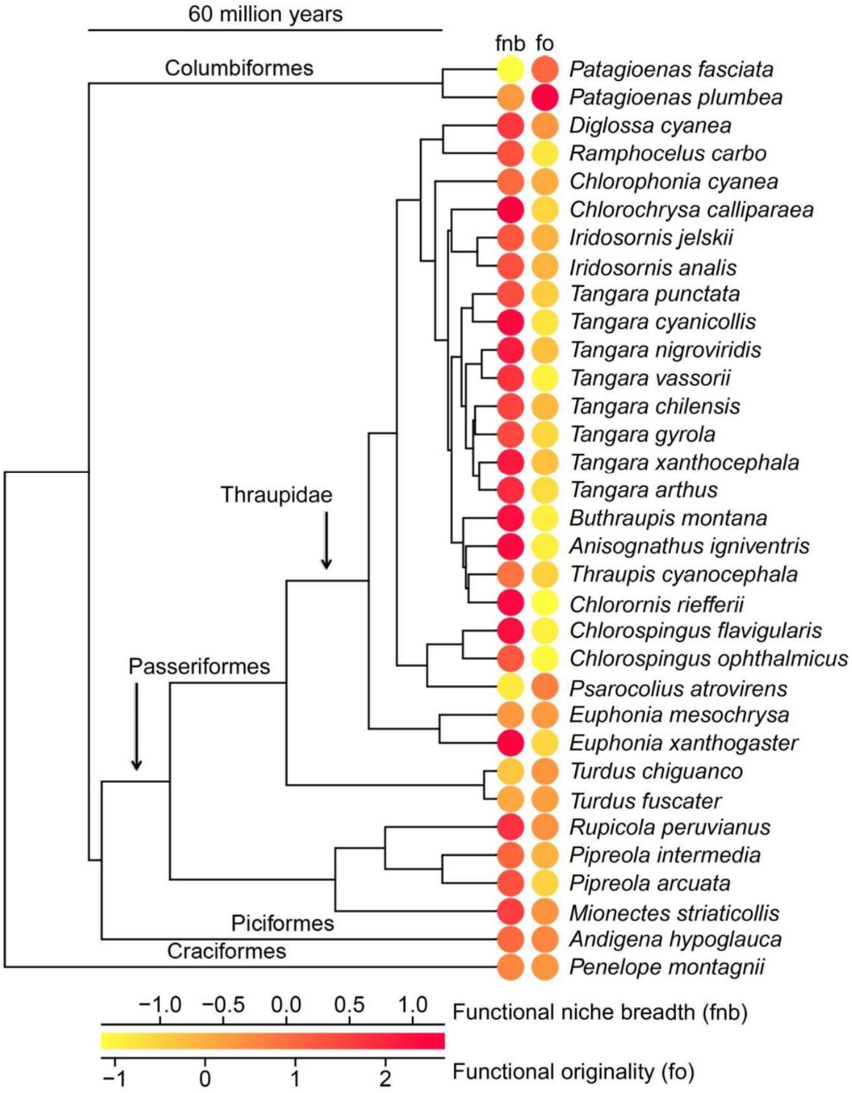

Figure 2.4. Functional niche breadth and functional originality across the avian phylogenetic tree. Light tips indicate low values, dark tips high values. High values of functional niche breadth, corresponding to a low degree of functional specialization, were found in most tanagers (family Thraupidae). The lowest functional niche breadth values were found in a pigeon (*Patagioenas fasciata*) and in an oropendola (*Psarocolius atrovirens*). Functional originality showed a similar pattern to functional niche breadth: tanagers were generally less functionally specialized than the other lineages. Values represent means across seasons.

RESULTS

Seasonal changes in plant trait spaces

We observed 52 fleshy-fruited plant species in the network at San Pedro (1500 m) and 51 plant species in the network at Wayqecha (3000 m). This resulted in a total of 99 unique plant species. In both networks, plant species were clustered in certain areas of the plant trait space, while a few species with extreme trait combinations determined the extent of the available plant traits in each season (Fig. 2.2). Functional richness and functional dispersion differed between seasons. In San Pedro, the first season was characterized by the highest values for functional richness and dispersion, whereas the second season had the lowest values (Fig. 2.2a). The network at Wayqecha showed similar patterns of seasonal variation (Fig. 2.2b).

Seasonal variation and phylogenetic signal in functional niche breadth and functional originality

Out of the 33 analyzed bird species, the 10 species with the highest values of functional niche breadth and thus the lowest degree of specialization within each season were all tanagers (family Thraupidae) (Fig. 2.3a, b). The pigeons *Patagioenas fasciata* and *Patagioenas plumbea*, the toucan *Andigena hypoglauca*, the oropendola *Psarocolius atrovirens* and the guan *Penelope montagnii* had consistently low values of functional niche breadth in the seasonal networks (Fig. 2.3a, b). Functional originality showed an inverse trend to functional niche breadth (Fig. 2.3b, c), and hence a similar pattern in terms of functional specialization. The lowest functional originality (and thus lowest seasonal specialization) was found in tanagers, whereas pigeons, the toucan, the oropendola and the guan had consistently high values (Fig. 2.3c). Consequently, species identity had a strong, statistically significant effect on functional niche breadth ($\chi^2 = 106.0$, $P < 0.01$) and functional originality ($\chi^2 = 100.7$, $P < 0.01$) and explained a large amount of the variation in both functional niche breadth (partial $R^2 = 0.41$) and functional originality (partial $R^2 = 0.39$). In contrast, season had no effect on functional niche breadth ($\chi^2 = 3.4$, $P = 0.49$, partial $R^2 = 0.01$) and functional originality ($\chi^2 = 3.8$, $P = 0.44$, partial $R^2 < 0.01$). Hence, species had similar degrees of functional specialization across seasons (*i.e.*, small standard errors in Fig. 2.3b, c).

The phylogenetic analysis detected a strong phylogenetic signal in both functional niche breadth ($\lambda = 0.71$, $P = 0.01$) and functional originality ($\lambda = 0.89$, $P < 0.01$, Fig. 2.4). Thus, closely related species had similar degrees of functional specialization, *e.g.*, tanager species had consistently high values of functional niche breadth and low values of functional originality.

Relationship between functional specialization and flexibility

Functional flexibility was negatively associated with functional niche breadth ($b = –0.21$, $R^2 = 0.17$, $P = 0.02$) and positively associated with functional originality ($b = 0.63$, $R^2 = 0.49$, $P < 0.01$) (Fig. 2.5). The relationship between functional flexibility and functional niche breadth was consistent with the expectation from both null models of randomized species interactions (Patefield: 95% CI range of *b* = –0.40 to 0.00; Vázquez: 95% CI range of *b* = –0.29 to 0.06). However, the relationship between functional originality and functional flexibility w as always stronger than in null models of randomized species interactions (Patefield: 95% CI range of *b* = 0.05–0.50; Vázquez: 95% CI range of *b* = 0.12–0.55).

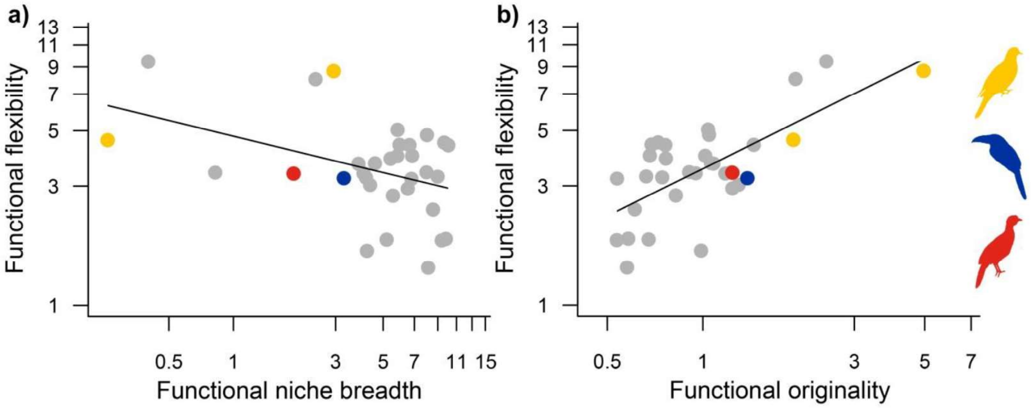

Figure 2.5. The relationship between functional flexibility across seasons and (a) seasonal functional niche breadth and (b) functional originality respectively. Fitted trend lines were derived from phylogenetic generalized least-squares models based on log-transformed values of the metrics. Points represent the 33 frugivorous bird species present in all four seasons of the plant–frugivore network at San Pedro and/or Wayqecha. The relationship in (a) was not different from the expectation of randomized species interactions, while the relationship in (b) was stronger than expected from null models. Both functional niche breadth and functional originality represent mean values across seasons. Functional niche breadth is negatively and functional originality positively related to functional specialization. The colored silhouettes illustrate the different bird orders; yellow for Columbiformes, blue for Piciformes, red for Craciformes and grey for Passeriformes.

DISCUSSION

We used two well-sampled plant–frugivore networks from the tropical Andes of south-east Peru to test whether (i) frugivorous bird species have similar degrees of functional specialization in different seasons; (ii) functional specialization of frugivorous birds is phylogenetically constrained; and (iii) bird species that are functionally specialized in a given season are flexible in switching to morphologically different resource types in other seasons. We found that both measures of functional specialization (*i.e.*, functional niche breadth and functional originality) showed little seasonal variation within species, but a strong phylogenetic signal and substantial variation across species. Moreover, we found that frugivores that are functionally specialized in a particular season are flexible in switching to other fruit resources in other seasons.

Seasonal variation in functional specialization

At our two study sites in the tropical Andes, the recorded changes in the functional diversity of the trait space of the fruiting plant community indicate that resources vary substantially among seasons (Fig. 2.2). This is in line with other studies on fruiting phenology in tropical rain forests (*e.g.*, Schaefer *et al.* 2002). Despite this variability in fruit resources, we found little seasonal variation in the functional niche breadth and functional originality of frugivorous bird species. Hence, frugivorous birds had a similar degree of functional specialization in different seasons throughout the year, despite the changing resource context.

Almost all bird species with a high functional niche breadth and a low functional originality were tanagers (Thraupidae), a family consisting of small-bodied, narrow-gaped frugivores (body mass <60 g). These species feed almost exclusively on small-sized fruits (Wheelwright 1985) such as those from *Miconia* plants that fruit over most time of the year (Hilty 1980). Compared to other frugivores, the large functional niche breadth (and low functional originality) of most tanagers results from consuming a high diversity of plant species within each season, mostly small-fruited plants that differ in plant height and crop mass. These plant species are often visited by large heterospecific flocks of tanagers that share similar types of fruit resources (Saracco *et al.* 2004).

In contrast to tanagers, species with a narrow functional niche breadth in a given season included two pigeons (*P. fasciata* and *P. plumbea*), an oropendola (*P. atrovirens*) and two thrushes (*Turdus chiguanco* and *Turdus fuscater*). These species, as well as a toucan (*A. hypoglauca*) and a guan (*P. montagnii*), also showed a high functional originality in the seasonal networks. Some of these species are among the largest frugivores in the community and differ widely in their bill and wing shapes. Compared to tanagers, they tend to consume large fruits (Wheelwright 1985) which are often less abundant and offered in the forest canopy rather than in the understorey (Flörchinger *et al.* 2010). Consequently, these frugivores are functionally more specialized on particular fruit types in a particular season and show a higher degree of functional originality than small-bodied species that preferentially exploit the most common resources in each season.

Phylogenetic signal in functional specialization

We found a strong phylogenetic signal in both functional niche breadth and functional originality. This indicates that species within specific phylogenetic lineages have a similar degree of functional specialization in plant–frugivore interaction networks. For instance, two pigeon species ranked among those species with the highest degree of functional specialization, whereas tanager species had a consistently high functional niche breadth and low functional originality. In mutualistic networks, phylogeny has been shown to influence species degree (*i.e.*, the number of partners) (Rezende *et al.* 2007, Kissling and Schleuning 2015) and species position within network modules (Schleuning *et al.* 2014). Our study further underlines the importance of the phylogenetic relatedness among species for unravelling patterns of functional specialization in ecological networks (Ibáñez *et al.* 2016).

Our findings have important implications for the robustness of ecological networks against species' extinctions or range shifts. If certain phylogenetic lineages are more likely to disappear than others, specific functional roles in a network will also disappear under the assumption that functional traits exhibit phylogenetic conservatism (Webb *et al.* 2002, Rezende *et al.* 2007, Díaz *et al.* 2013). Moreover, a high degree of functional specialization (*e.g.*, of pigeon or toucan species) might reflect a low functional redundancy as the loss of these species might not be compensated by other species (Dehling *et al.* 2016). These species might be considered to play a keystone role for the maintenance of community structure and ecosystem functioning (Mello *et al.* 2015). Thus, a strong phylogenetic signal in functional specialization may render the interaction networks susceptible to the loss of species with unique functional roles. This expectation is corroborated by studies showing that the loss of large seed dispersers from tropical forests leads to severe changes in plant community dynamics and forest structure (Galetti *et al.* 2013, Dirzo *et al.* 2014).

Functionally specialized species are most flexible in resource choice

We found that functional niche breadth was negatively and functional originality positively related to functional flexibility. Hence, birds with a high degree of functional specialization within seasons showed a high flexibility to switch between plant resources with different traits across seasons. We tested both relationships against two types of null models. Although the relationship between functional originality and flexibility was stronger than expected from both null models, the relationship between functional niche breadth and flexibility was not. As the measure of functional niche breadth does not account for differences in the interaction frequencies between species, it might be particularly sensitive to sampling effects because frequently observed species will tend to have a larger functional niche breadth than rarely observed species. This is also corroborated by the close relationship between species degree and functional niche breadth, indicating that this metric is to a large extent driven by the number of resource species recorded for each consumer species. In contrast, the measure of functional originality accounts for interaction frequencies between species and the community context and is therefore less prone to sampling effects. We propose that functional originality is therefore more suitable for comparative studies of functional specialization in ecological communities.

The positive relationship between functional specialization within seasons and flexibility across seasons is related to the morphological characteristics of the functionally most specialized frugivore species. The highest functional specialization was observed for relatively large-bodied frugivores with rather large bills (*e.g.*, pigeon, toucan, oropendola, guan and thrush species). These species preferably feed on large fruits (*e.g.*, *Clusia alata*, Clusiaceae, or *Ruagea subviridiflora*, Meliaceae) because feeding on large resource types might optimize their foraging efficiency (Corlett and Primack 2011). However, the preferred large fruits are not constantly available throughout the year which forces large frugivores to seasonally switch to other types of fruits, *e.g.*, to fruits of medium size such as *Podocarpus oleifolius* (Podocarpaceae) and *Hedyosmum tepuiense* (Chloranthaceae). Hence, large frugivores must be relatively flexible to switch to other resources in response to fluctuations in fruit resource availability. In contrast, bird species with narrow bills are less flexible in fruit choice, but are able to interact with a constantly diverse community of small-fruited plant species in the forest understorey and canopy throughout the year.

Trait matching between resource and consumer species seems to be a widespread phenomenon in ecological networks (*e.g.*, Wheelwright 1985, Woodward and Warren 2007, Stang *et al.* 2009, Maglianesi *et al.* 2014, Dehling *et al.* 2016). Hence, interaction systems other than plant–frugivore networks might also show a positive relationship between functional specialization and flexibility of consumer species. For instance, insect and bird pollinators with adaptations to exploit nectar from long flower tubes are also able to visit short flowers, whereas species with a short proboscis or beak are constrained to visit short flowers (Stang *et al.* 2009, Maglianesi *et al.* 2015). Similarly, large predators are able to feed on prey species of different size, whereas smaller predators are restricted to small prey species (Wilson 1975, Woodward and Warren 2007). Consistent with our findings, this suggests that the consumers that are functionally most specialized in a given spatial or temporal context may, nevertheless, be the most flexible in responding to resource fluctuations. To measure how a species' dietary preference changes over time or in space, we here propose the metric of functional flexibility. This metric may be better suited to quantify the dependence of consumers on specific resources than measures of functional specialization that do not account for the temporal or spatial variability in resource availability.

CONCLUSION

Our findings have two important implications. First, our results confirm that specific bird species and specific phylogenetic lineages fulfill particular functional roles in plant–frugivore networks. Loss of these species will probably lead to a loss of functionality from ecological communities that cannot directly be compensated by other species. Second, we found that bird species that are temporarily specialized on particular resource types are able to switch to different resource types in response to resource fluctuations. This flexibility of consumer species to respond to changes in resource availability may be an important, but so far largely neglected mechanism to stabilize ecological networks between resource and consumer species. Flexibility in resource choice may also foster the adaptability of ecological networks to species turnover in ecological communities as a consequence of global change.

AUTHORS' CONTRIBUTIONS

I.M.A.B., W.D.K., D.M.D. and M.S. conceived the general ideas and designed the research. D.M.D. and I.M.A.B. collected the data. I.M.A.B. performed the analysis with input from W.D.K., D.M.D. and M.S. All authors discussed the results. I.M.A.B. wrote the first draft of the manuscript with input from W.D.K., D.M.D. and M.S. All authors commented on the manuscript, including revisions, and approved the final version of the manuscript.

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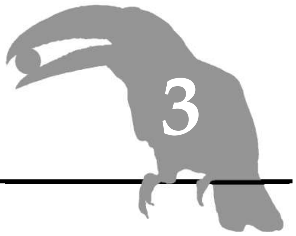
DATA ACCESSIBILITY

Data on seasonal networks and plant traits are archived in the Senckenberg Data & Metadata Repository https://doi.org/10.12761/sgn.2017.1 (Dehling 2017).

SUPPLEMENTARY MATERIALS

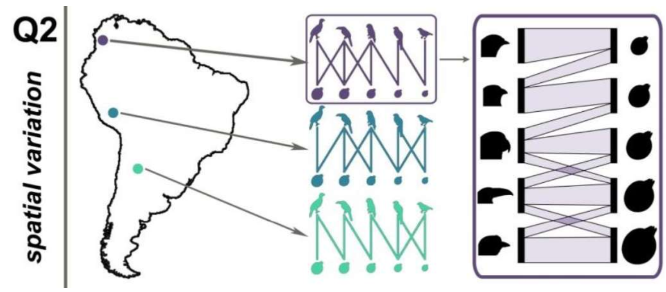
The following supplementary materials are available from pp. 117–121:

Figure S2.1	Seasonal interaction networks at San Pedro and at Wayqecha in Manu, Peru.
Figure S2.2	Plant trait space.



Chapter 3

Morphological trait matching shapes plant-frugivore networks across the Andes



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MORPHOLOGICAL TRAIT MATCHING SHAPES PLANT-FRUGIVORE NETWORKS ACROSS THE ANDES

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SUMMARY

Interactions between resource and consumer species are organized in ecological networks. Species interactions in these networks are influenced by the functional traits of the interacting partners, but the generality of trait-based interaction rules and the relationship between functional traits and a species' specialization on specific interaction partners are not yet understood. Here we combine data on eight interaction networks between fleshy-fruited plants and frugivorous birds sampled across the tropical and subtropical Andean range. We test which combinations of morphological plant and animal traits determine trait matching between resource and consumer species in these networks. In addition, we test which of the morphological traits influence functional specialization of plant and bird species. In a meta-analysis across network-specific fourth-corner analyses, we found that plant-animal trait pairs related to size matching (fruit size-beak size) and avian foraging behavior (plant height-wing shape and crop mass-body mass) were positively related in these networks. The degree of functional specialization on specific interaction partners was positively related to crop mass in plants and to the pointedness of the wing in birds. Our findings show that morphological trait matching between fleshy-fruited plants and frugivorous birds is a general phenomenon in plant-frugivore networks across the Andes and that specific plant and bird traits can be used to approximate the degree of functional specialization. These insights into the generality of interaction rules are the base for predictions of species interactions in ecological networks, for instance in novel communities in the future, and can be applied to identify plant and animal species that fulfill specialized functional roles in ecological communities.

INTRODUCTION

Species interactions in ecological communities are often influenced by the degree of trait matching between potential partners (Wheelwright 1985, Woodward and Warren 2007, Stang *et al.* 2009, Dehling *et al.* 2014b, Maglianesi *et al.* 2015). For instance, size matching describes the phenomenon that large predators tend to interact with large prey species, whereas small predators are usually constrained to small-sized prey species (Cohen *et al.* 1993, Woodward and Warren 2007, notable exceptions include large marine mammals, Tucker *et al.* 2016). It should therefore, in principal, be possible to infer interaction rules from the traits influencing the matching of potential partners (Gravel *et al.* 2013) since the likelihood of interactions increases with the degree of trait matching in many interaction systems (Levey 1987). Knowledge about trait matching rules that govern the interactions between resource and consumer species can be used to make projections about which pairs of species are likely to interact in current or potential future communities (Morales-Castilla *et al.* 2015, Bartomeus *et al.* 2016). The first step towards such projections is to identify general interaction rules based on matching traits across interaction networks sampled at different localities (Kissling and Schleuning 2015).

Matching traits also define a species' functional role in interaction networks (Schleuning *et al.* 2015). This follows from the concept of the Eltonian niche (Elton 1927, Chase and Leibold 2003), which assumes that species that interact with different sets of interaction partners fulfill different functional roles in ecological communities. In interaction networks, the functional role of species is therefore most accurately described by the functional traits of their interaction partners (Dehling *et al.* 2016, Bender *et al.* 2017). Since species differ widely in their functional roles, *e.g.*, in their degree of specialization on specific partners (Olesen *et al.* 2011a, Waser and Ollerton 2006), species that interact with a set of species with which few other species interact are functionally specialized in respect to the co-occurring species (Dehling *et al.* 2016). These functional specialists can provide ecological functions that no or few other species can provide and may be considered especially important for the interaction network and the entire ecosystem (Mello *et al.* 2015, Sebastián-González 2017). Since data on species interactions are notoriously difficult to record (Jordano 2016b), it would be desirable to approximate the degree of functional specialization of plant and animal species directly from their own morphological traits. One possibility to get a more general understanding of the types of species that contribute specialized functional roles to ecological networks is therefore to identify matching traits that are associated with a high degree of functional specialization across networks from different localities.

Matching traits have been previously identified in studies of mutualistic plant-animal interaction networks (Wheelwright 1985, Jordano 1987, Stang *et al.* 2009, Dehling *et al.* 2014b, Maglianesi *et al.* 2015) and can be categorized into two groups. The first group consists of traits which relate to the matching between plant and animal size (size matching) and correspond, for instance, to a matching between flower or fruit size and the respective animal organs, such as proboscis or bill size (Wheelwright 1985, Stang *et al.* 2009, Garibaldi *et* *al.* 2015, Sebastián-González *et al.* 2017). Second, matching traits can be related to the foraging behavior of consumers and are, for instance, related to traits associated with animal mobility, such as avian wing shape, and the location of plant resources, such as forest stratum (Moermond and Denslow 1985, Schleuning *et al.* 2011). Additionally, consistent with the theory of optimal foraging, large species require energy-rich resources (Belovsky 1997, Petchey *et al.* 2008). Therefore, animals with a large body size tend to prefer energy-rich resources (Krebs and Davies 1993). Since different traits, and the combination of these traits, influence the matching of species in interaction networks, the same traits may also influence the degree of functional specialization within networks (Dehling *et al.* 2016) and may be used to identify species with important functional roles in networks (Sebastián-González 2017). Most previous work on trait matching and functional specialization in mutualistic networks has focused on specific localities and on the consumer perspective (*e.g.*, Dehling *et al.* 2016, Bender *et al.* 2017).

Here, we conduct a large-scale analysis across mutualistic seed-dispersal networks to compare the importance of different pairs of matching traits for both the degree of trait matching and the functional specialization of plant and animal species in these networks. To this end, we combined eight interaction networks from five different countries stretching the tropical and subtropical Andean range to identify general interaction rules in plant-frugivore networks. The Andean mountain range is a global diversity hotspot for both fleshy-fruited plants (Jansson and Davies 2008) and frugivorous birds (Kissling *et al.* 2009). This diversity, in combination with the wide geographical range of the Andes, makes it an ideal region to test the generality of trait matching and to identify functional traits that determine functional specialization in plant-frugivore networks.

Specifically, we ask (i) which trait pairs influence the matching between plants and animals, and (ii) which traits influence the functional specialization of plants and animals across networks. We expect that (i) trait pairs related to size matching will be more important in shaping plant-animal interactions than foraging-related trait pairs, because size matching imposes direct constraints on the likelihood of interactions (Wheelwright 1985, Sebastián-González *et al.* 2017). In addition, we expect that (ii) large-fruited plants and large-billed bird species show the highest level of functional specialization across networks because these species are reciprocally specialized on each other (Moermond and Denslow 1985, Wheelwright 1985) and are relatively rare in the respective communities (Wheelwright 1988).

MATERIALS AND METHODS

Interaction networks

We combined data from interaction networks between fleshy-fruited plants and frugivorous birds collected at eight different locations across the Andes. The eight networks included two networks from Colombia, two networks from Ecuador, two networks from Peru, one network from Bolivia and one network from Argentina (Fig. 3.1). The networks cover an elevation range from 1000 to 3000 m a.s.l. (hereafter "m") and extend from 4.7°N to 26.5°S, covering a large portion of the tropical and subtropical Andean range. All networks were collected in near-natural forest, *i.e.*, networks from highly fragmented or intensively disturbed forests were not considered in the analyses because the importance of species traits may be weakened in disturbed, impoverished communities (Saavedra *et al.* 2014).

All networks comprise information on the frequency of visits of frugivorous bird species on fleshy-fruited plant species (weighted networks). We only included true seed-dispersal events in the analyses that correspond to fruit swallowing or carrying-away. Collection effort was similar among networks (range of sampling hours: 300 - 960, mean = 606, standard deviation = 224), but the number of observed interaction events varied among networks (range of observed interaction events: 241 - 4988, mean = 1447, SD = 1539). The network sampled in Bolivia was the smallest network comprising 19 plant and 22 bird species. The largest network from Peru comprised 52 plant and 61 bird species (Fig. 3.1). Overall, we analysed 227 plant species interacting with 180 bird species in 11,578 interaction events. The most species rich plant genus was *Miconia* (Melastomataceae) with 39 species. The largest group of birds were the tanagers (genus *Tangara*, 19 species, family Thraupidae). A more detailed description of the sampling of each network is given in Supplement 3.1.

To assess the sampling completeness of each network (Chacoff *et al.* 2012), we generated accumulation curves of the observed bird richness and the number of interaction pairs (link richness) and calculated the asymptotic bird and link richness based on the Chao richness estimator (Oksanen *et al.* 2015). All interaction networks were similarly well sampled, as indicated by the saturating trends in the accumulation curves (Figs. S3.1, S3.2). Bird richness approached the asymptotic richness in all networks (Fig. S3.1).

Morphological traits

Morphological traits were collected for all plant and bird species observed in the interaction networks. We selected traits that were identified as key matching traits in plant-frugivore networks in the Peruvian Andes (Dehling *et al.* 2014b). Plant traits included fruit diameter (mm), fruit length (mm), plant height (m) and crop mass (g, number of fruits per plant multiplied by mean individual fruit mass). Plant traits were measured in the field on several plant individuals per species. Bird traits included bill width (mm), bill length (mm), wing shape (*i.e.*, Kipp's index as a measure of the pointedness of the wing) and body mass (g). Kipp's index was calculated by dividing the Kipp's distance (the distance between the tip of the first secondary and the wing tip, measured on the folded wing, Leisler and Winkler 1991) by wing length. A high Kipp's index indicates a wing shape which enables birds to fly over long distances, whereas a low Kipp's index indicates rounded wings that are especially suited for high maneuverability in dense vegetation (Rayner 1988). Bird traits were

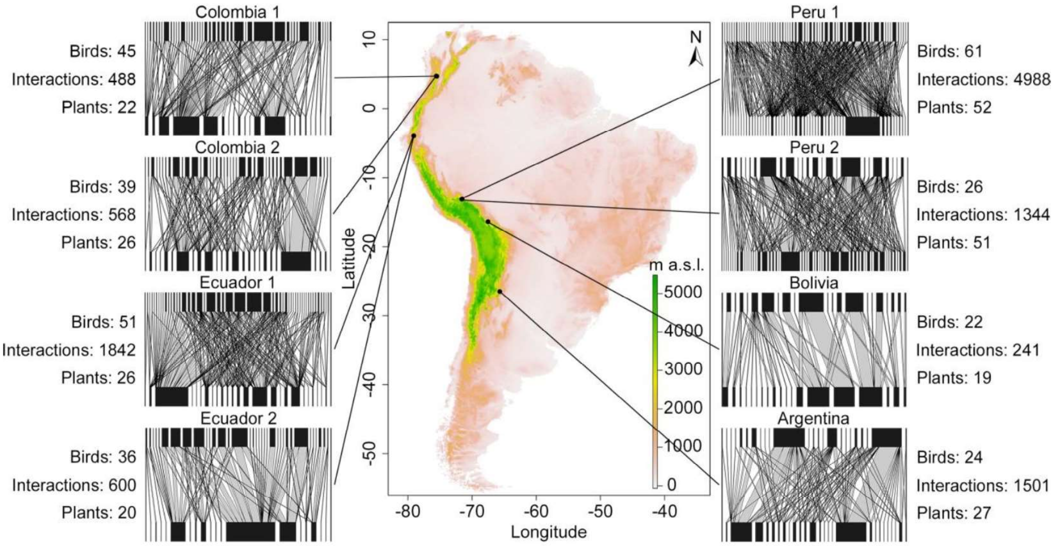

Figure 3.1. Overview of the eight interaction networks sampled across the Andes. Networks represent interactions between fleshy-fruited plants (bottom boxes) and frugivorous birds (top boxes): Colombia 1 (2000 m a.s.l.), Colombia 2 (2500 m), Ecuador 1 (1000 m), Ecuador 2 (2000 m), Peru 1 (1500 m), Peru 2 (3000 m), Bolivia (2500 m) and Argentina (1000 m). Interactions between species are indicated by lines between boxes; box size and line width indicate the frequency of frugivore visits. For each network, the number of bird species, plant species and the total number of observed interaction events is given. The lines connect the networks to the location in South America where they were collected.

measured on several museum specimens. Trait data for all eight interaction networks were collected using the same methodologies.

We log-transformed plant traits (fruit diameter, fruit length and crop mass) and bird traits (bill width, bill length and body mass) prior to the analysis to approximate a normal distribution of trait data. Plant height and Kipp's index were not log-transformed since these traits did not deviate from a normal distribution.

Trait matching

In order to identify which trait combinations shape plant-animal matching across sites, we used a modified version of the fourth-corner analysis. The fourth-corner analysis was initially proposed to measure and test the relationship between species traits and environmental variables (Legendre *et al.* 1997, Dray and Legendre 2008). Dehling *et al.* (2014) modified this approach to test the relationship between plant traits and bird traits. They used the species interaction matrix **L** between plants and birds (plant species*bird species, unit: interaction strength, the proportion of visits of a frugivore species to each plant species, Bascompte and Jordano 2007) to compare a matrix **R** of plant traits (plant species*plant traits) with a matrix **Q** of bird traits (bird species*bird traits). The objective of the fourth corner analysis is then to estimate the parameters of a fourth matrix **X** (plant traits* bird traits) that quantifies the correlation between pairs of plant and bird traits.

For each network, we tested four pairs of plant and bird traits (Dehling *et al.* 2014b): fruit diameter vs. bill width, fruit length vs. bill length, plant height vs. Kipp's index, crop mass vs. body mass. We used a null model (*i.e.*, testing for the null hypothesis **X** = 0) to test whether the traits of plants and birds were significantly correlated (*i.e.*, **X** ≠ 0). Null model testing is complex because it involves the relationships of the interaction matrix **L** to both plant traits **R** and bird traits **Q**. A proposed solution is to first remove the relationship between plant traits and observed interactions by permutating plant identities in the interaction matrix **L** and then to remove the relationship between bird traits and the observed interactions by permutating the bird identities in the interaction matrix **L** (Dray and Legendre 2008, Ter Braak *et al.* 2012). This approach has been implemented as permutation model type 6 (fourthcorner in 'ade4' package in R, Dray and Legendre 2008), which combines the output of model type 2 (plant species of the interaction matrix are permuted) and model type 4 (bird species of the interaction matrix are permuted) and selects the larger of the two *P* values of the two permutation types (Ter Braak *et al.* 2012).

We extracted the Pearson's correlation coefficients *r* for each trait pair from the matrix **X** of the individual fourth-corner analyses for each of the eight networks. To generalize the individual fourth-corner results for the entire Andean range, we performed a meta-analysis (metacor.DSL in 'metacor' package in R, Laliberté 2011) across the Pearson's correlation coefficients *r* of the eight individual fourth-corner analyses. Prior to the meta-analysis, we applied Fisher's z-transformation to the correlation coefficients to approximate a normal distribution of *r* (escalc in 'metafor' package in R, Viechtbauer 2010). We performed this meta-analysis in two ways. First, we defined the square-root of the total number of interactions observed in each network as sample size for each network and weighted the meta-analysis by this measure of sampling effort since the accuracy of fourth-corner correlations in network analyses increases with the total number of observed interactions (see Appendix S2 in Dehling *et al.* 2014b). Second, we quantified the sampling completeness of each network by dividing the number of observed links by the asymptotic link richness, based on the Chao estimator, and weighted the meta-analysis by sampling completeness.

Functional specialization

As a measure for functional specialization, we calculated the functional originality, the extent to which species interact with partners that only few other species interact with (Dehling *et al.* 2016) for all plant and bird species. First, plant traits of all networks were combined in a single trait matrix. Pairwise Mahalanobis distances between all plant species were calculated and used in a Principal Coordinates Analysis (PCoA). This analysis resulted in four axes that represent the total variation in plant traits across all networks. Second, to determine the functional originality of bird species in each network, we selected all plant species that a specific bird species interacted with in the respective network. We averaged the PCoA coordinates of these plant species weighting them by the respective interaction strength (Bascompte and Jordano 2007). This resulted in a weighted interaction centroid of a bird species in plant trait space (Dehling *et al.* 2016). Third, we calculated the community centroid as the unweighted mean of the interaction centroids of all bird species present in the respective network. Functional originality was then measured as the Euclidian distance between the interaction centroid of a specific bird species and the community centroid (Dehling *et al.* 2016). A high functional originality value indicates that a bird interacted mostly with plant species characterized by traits that only few other bird species interacted with. We repeated the analogous procedure for the plant species and here defined the functional originality of plant species in a four-dimensional bird trait space based on the PCoA coordinates derived from bill width, bill length, wing shape and body mass. Functional originality values of plant and bird species were log-transformed to approximate a normal distribution of values. These values were scaled to a mean of 0 and a standard deviation of 1 across networks, which ensures that model estimates were comparable between plant and bird species.

We aimed at identifying which plant and bird traits were most closely associated with species' functional specialization. To identify the relative importance of the four functional plant (fruit diameter, fruit length, plant height and crop mass) and bird traits (bill width, bill length, wing shape and body mass), we fitted linear mixed-effect models ('lme4' package in R, Bates *et al.* 2015) across all species in the eight networks, separately for plants and birds. In the two overall models, we thus fitted species' functional originality as the response variable and the four functional plant or bird traits as predictor variables. Prior to model fitting, functional traits of plants and birds were standardized to a mean of 0 and a standard deviation of 1 across networks which ensures that model estimates are comparable among traits. All models included 'network identity'as a random effect to account for the fact that estimates of functional originality were derived from different networks. In addition, 'species identity' was included as a random effect because a species could occur in more than one network. We initially included also higher-level taxonomic information (*i.e.*, genus and family). However, because this resulted in qualitatively identical results we omitted these terms from the final models in the interest of parsimony. In order to correct for differences in sampling effort among networks, we weighted estimates of functional originality for each species by sampling effort, *i.e.*, the square-root of the total number of interactions observed in the respective network.

To identify the best model, we first fitted all possible submodels (dredge in 'MuMIn' package in R, Barton 2016) of the global models. To avoid collinearity among predictors, we constrained the resulting set of models to exclude models where traits with a correlation coefficient higher than $|0.5|$ were combined. For plant species, fruit diameter and fruit length ($r = 0.74$) and crop mass and fruit diameter ($r = 0.54$) were highly correlated, while for bird species this was the case for bill width and bill length ($r = 0.90$), bill width and body mass ($r = 0.85$) and bill length and body mass ($r = 0.84$). We compared the resulting set of sub-models according to the Akaike information criterion corrected for small sample size (AICc, Burnham and Anderson 2002). We obtained the variable importance (*i.e.*, the summed

Akaike weights of all models including the respective predictor variable) and weighted mean model coefficients across all models with a ΔAICc value smaller than 2 relative to the best model with the lowest AICc value (full model estimates derived from model.avg in 'MuMIn' package in R, Barton 2016).

RESULTS

Trait matching

The meta-analysis across the eight Andean interaction networks, weighted by sampling effort, showed a strong signal of trait matching for all pairs of plant and frugivore traits (Fig. 3.2). Contrary to our expectation, there was no major difference in the correlation strength between traits related to size matching and foraging strategy. Fruit diameter vs. bill width ($r = 0.32$, $P < 0.001$) and plant height vs. wing shape ($r = 0.33$, $P < 0.001$) showed the strongest correlations. The correlations between fruit length vs. bill length ($r = 0.26$, $P < 0.001$) and crop mass vs. body mass ($r = 0.21$, $P = 0.02$) were slightly weaker. The meta-analysis weighted by sampling completeness showed qualitatively identical results (Table S3.1). In the individual networks, correlation coefficients between the pairs of matching traits were more variable than in the meta-analyses (Fig. S3.3). Except for the crop mass-body mass relationship, trait correlations were always positive, consistent with the overall signal of trait matching across networks.

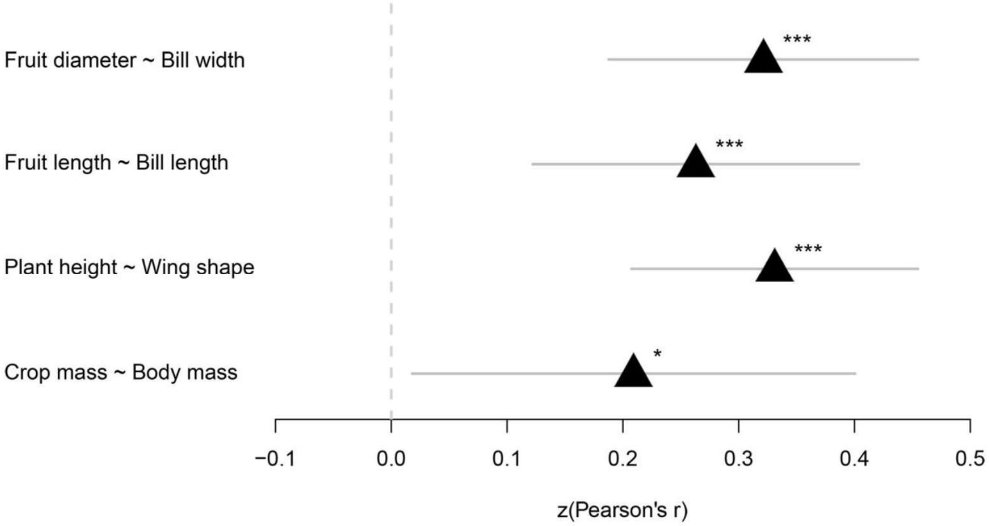

Figure 3.2. Matching of plant and frugivore traits across eight Andean networks. Results are derived from a meta-analysis of fourth-corner correlations between plant-frugivore trait pairs, weighted by sampling effort. Triangles indicate the mean of z-transformed Pearson's correlation coefficients *r*. Grey lines indicate the estimated variance of correlation coefficients. Asterisks indicate the level of significance for each trait pair (***, $P < 0.001$; *, $P < 0.05$).

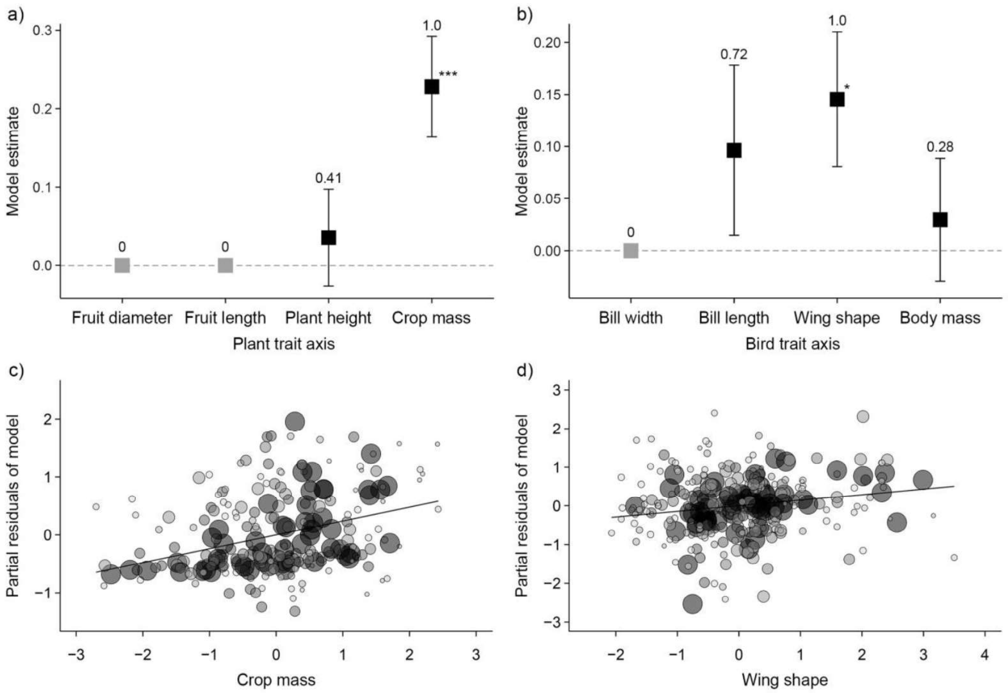

Figure 3.3. Relationships between morphological traits and species' functional specialization in (a) plants and (b) frugivorous birds and partial residual plots for the significant relationships in (c) plants and (d) birds, respectively. Results are obtained from mixed-effects models with functional specialization of plants or birds as response variable, and traits as predictor variables (plants: fruit diameter, fruit length, plant height and crop mass; birds: bill width, bill length, wing shape and body mass), including 'species identity' and 'network identity' as random effects. Functional specialization was measured by functional originality, *i.e.*, the extent to which species interact with partners characterized by traits that only few other species interact with. Shown are results from model-averaged coefficients across a subset of best models (ΔAICc < 2). Grey estimates indicate variables that were not included in the set of best models. In (a) and (b), the relative variable importance is given and asterisks indicate the level of significance of the model-averaged estimates (***, $P < 0.001$; *, $P < 0.05$). In (c) and (d), each dot represents a plant or a bird species in a specific network. Dot size and the degree of shading are proportional to the square-root number of observed interactions in the respective network.

Functional specialization

In the eight analyzed networks, the highest degrees of functional specialization were found in the plant species *Alchornea grandiflora* (Euphorbiaceae, Colombia 1), *Oreopanax caricifolium* (Araliaceae, Colombia 2), *Schefflera sp*. (Araliaceae, Ecuador 1), *Isertia laevis* (Rubiaceae, Ecuador 2), *Endlicheria sp*. (Lauraceae, Peru 1), *Clusia elliptica* (Clusiaceae, Peru 2), *Symplocos arechea* (Symplocaceae, Bolivia) and *Duranta serratifolia* (Verbenaceae, Argentina). The most functionally specialized bird species in the networks were the Golden-headed Quetzal (*Pharomachrus auriceps*, Trogonidae, Colombia 1), Masked Trogon (*Trogon personatus*, Trogonidae, Colombia 2), Ruddy Pigeon (*Patagioenas subvinacea*, Columbidae, Ecuador 1), Emerald Toucanet (*Aulacorhynchus prasinus*, Ramphastidae, Ecuador 2), Chestnut-tipped Toucanet (*Aulacorhynchus derbianus*, Ramphastidae, Peru 1), Blue-banded Toucanet (*Aulacorhynchus coeruleicinctis*, Ramphastidae, Peru 2), Blue-and-black Tanager (*Tangara* *vassorii*, Thraupidae, Bolivia 2), and Crested Becard (*Pachyramphus validus*, Tityridae, Argentina). The majority of the functionally most specialized bird species did *not* belong to the Passeriformes although these are usually the most common birds in seed dispersal networks.

We identified specific plant and bird traits that explained the differences in functional specialization, *i.e.*, the functional originality of species, among plant and bird species (Fig. 3.3). For plants, we identified two models with a ΔAICc value smaller than 2; the best model included only crop mass (ΔAICc = 0) and the second-best model included crop mass and plant height (ΔAICc = 0.69). In the averaged model, crop mass was positively related to the degree of functional originality of plants ($b = 0.23$, $P < 0.01$), whereas the effects of plant height ($b = 0.04$, $P = 0.57$) was not significant (Fig. 3.3a). For birds, two models had a ΔAICc value smaller than 2; the best model included wing shape and bill length (ΔAICc = 0) and the second-best model included wing shape and body mass (ΔAICc = 1.84). In the averaged model, the pointedness of the wing ($b = 0.15$, $P = 0.03$) was positively related to the degree of functional originality of birds, whereas the effects of bill length ($b = 0.10$, $P = 0.24$) and body mass ($b = 0.03$, $P = 0.62$) were not significant (Fig. 3.3b).

DISCUSSION

We combined eight plant-frugivore interaction networks, sampled along the Andean range, to identify functional traits that determine the degree of trait matching and functional specialization of plants and animals. We found that plant and animal traits related to size matching (fruit size-beak size) and animal foraging (plant height-wing shape and crop mass-body mass) were important in shaping plant-frugivore interaction networks across the Andes. Specific plant and animal traits were only weakly associated with species' functional specialization across networks. Nevertheless, we detected that plant crop mass was positively related to the degree of functional specialization of plants, while the pointedness of the wing was positively related to the degree of avian functional specialization.

Trait matching across the Andes

Our meta-analysis across eight Andean interaction networks showed that plant and animal traits, both related to size matching and to animal foraging, determined the matching of plant and animal species in plant-frugivore networks. The importance of traits related to size matching is well studied in ecological interaction networks (Wheelwright 1985, Stang *et al.* 2009, Garibaldi *et al.* 2015). For instance, bird-dispersed fruits strongly depend on bird species that have a sufficiently large gape width that enables them to swallow the fruit (Levey 1987), insect and bird pollinators with a short proboscis or bill are constrained to visit short flowers (Stang *et al.* 2009, Maglianesi *et al.* 2015), and small predators are usually unable to feed on large prey (Cohen *et al.* 1993, Woodward and Warren 2007). This has resulted in the hypothesis that size matching is a general principle in ecological interactions (Olesen *et al.* 2011b). The results from our meta-analysis support this hypothesis.

In contrast to our initial expectation, we found that traits related to foraging strategies of frugivorous birds, were equally important as trait pairs related to size matching in shaping interaction networks. The shape of a bird's wing is related to its movement capacity and maneuverability (Rayner 1988). Rounded wings allow a bird to move in dense forest understory, while birds with pointed wings are better equipped for long-distance flights and foraging in the canopy (Moermond and Denslow 1985). Wing shape therefore directly influences where a bird species encounters fruits while foraging (Schaefer *et al.* 2002). In our networks, bird species with rather pointed wings were, for example, the Golden-headed Quetzal (*Pharomachrus auriceps*, Trogonidae) and the Masked Trogon (*Trogon personatus*, Trogonidae). These birds were also among the most functionally specialized birds in the networks. Wing shape has likewise been shown to influence flight maneuverability and foraging behavior in bats (Norberg and Rayner 1987, Swartz *et al.* 2003). This suggests that the influence of wing shape on interaction networks is a general phenomenon across different types of plant-frugivore networks.

The relationship between crop mass and body mass is consistent with the theory of optimal foraging (Krebs and Davies 1993, Belovsky 1997, Petchey *et al.* 2008). According to this theory, large bodied birds need to feed on energy-rich resources to meet their energetic demands (Corlett and Primack 2011). Large-bodied frugivores therefore feed mostly on plants with a large crop mass, which offer a high amount of resources accumulated in one place, while small bodied frugivores tend to visit several individuals of plants with small crops (Dehling *et al.* 2014b, Howe 2016, Muñoz *et al.* 2017).

Despite the overall significant relationships between all trait pairs, the degree of trait matching differed among networks, especially in the case of the crop mass-body mass relationship. These differences could be due to differences in sampling effort and completeness among networks as the likelihood to detect trait matching increases with the number of observed interaction events (Dehling *et al.* 2014b). Moreover, we compared communities that differed widely in their species pools. For instance, maximum body size varied from 706 g (Peru 1 & 2, Bolivia) to 1180 g (Ecuador 2). Depending on the degree of trait variation and the dominance of specific trait values in a community, the detectability of trait matching may differ among networks (Dehling *et al.* 2014b). For instance, we would expect that the degree of trait matching is weakened in modified ecological communities that are dominated by small-bodied species (Saavedra *et al.* 2014). Moreover, consumer species can respond flexibly to fluctuations in resource availability (Bender *et al.* 2017), which will also result in fluctuations in the degree of trait matching between plant and animal species. This variability does not question the overall importance of trait matching, here exemplified across the Andean range, but cautions against generalizations from species-rich to species-poor ecosystems.

The relationship between functional traits and functional specialization

While we expected that large-fruited plants and large-billed bird species show the highest level of functional specialization across networks, we found that the relationship between functional specialization and plant and bird traits was overall weak across the range of studied networks. Nevertheless, we were able to identify a single plant trait (crop mass) and a single bird trait (wing shape) that were significantly associated with functional specialization. Our results indicate that plants that produced a large crop mass attracted a morphologically distinct set of bird species compared to other plant species in the community. Since phylogenetically unrelated plant species were the functionally most specialized in each network, this finding suggests that specific trait values, rather than species taxonomy, are associated with plant functional specialization. Plant species with large crops might especially attract large-bodied birds (Dehling *et al.* 2014b) that rely on such resources to meet their high energy demands (Krebs and Davies 1993). For instance, *Clusia elliptica* (Clusiaceae) interacted with the Blue-banded Toucanet (*Aulacorhynchus coeruleicinctis*), one of the largest frugivorous birds in the Peruvian bird community at 3000 m (Peru 2, body mass = 208 g). In contrast, plants with small fruit crops are mostly visited by bird species with less distinct traits, such as the many tanager species. Hence, our findings suggest that plants with large crops attract, and potentially require, functionally more distinct seed dispersers than plants with small crops.

Bird species with pointed wings were identified to visit the most distinct set of plant species in the community. Across networks, bird species with a high degree of functional specialization were scattered across different taxonomic groups, indicating that functional specialization is related to specific trait values largely independent of species' phylogeny. Bird species with pointed wings usually feed in the canopy of the forest and are able to fly long distances (Moermond and Denslow 1985, Dehling *et al.* 2014b). Due to their flight ability, these species can provide long-distance dispersal to plant communities (Böhning-Gaese *et al.* 2006). This is the reason why such species are particularly important for connecting forest patches in fragmented landscapes (Müller *et al.* 2014). According to our analyses, these species also provide seed-dispersal functions to specific types of plant species as they were functionally most specialized. While previous studies have highlighted that the loss of large-bodied animal species from tropical forests has severe consequences for the plant community (Galetti *et al.* 2013, Vidal *et al.* 2013), our results indicate that the loss of bird species with pointed wings might similarly have severe functional consequences for tropical forests.

Since we found a high degree of trait matching between individual trait pairs, we expected that functional specialization of plants and birds was determined by corresponding matching traits (*e.g.*, large-fruited plants and large-billed bird species). However, the identified plant and bird traits, crop mass and wing shape, did not belong to the same trait pair, nor was there a strong correlation between plant height and crop mass (n = 243 species, r = 0.34) or wing shape and body mass (n = 304 species, r = 0.22). This indicates that there are important differences in the types of traits that are associated with functional specialization in plant and bird communities. In plant communities, those species that invest comparatively little energy into their fruits are mostly dispersed by similar types of often small-bodied bird species (McKey 1975, Kessler-Rios and Kattan 2012). In contrast, the few plant species that invest into a large crop mass and attract a functionally distinct group of frugivorous birds might benefit from long-distance dispersal or from dispersal to different locations relative to other plant species in the community (Howe and Smallwood 1982). In bird communities, canopy-foraging birds with pointed wings follow a different strategy of fruit tracking than species with more rounded wings as they are able to move over longer distances and are, thus, able to reach specific types of fruit (Lindberg and Olesen 2001, Moermond and Denslow 1985). These bird species are likely to provide particularly valuable seed-dispersal functions to plant communities.

CONCLUSION

We found across a large geographic range that traits related to size matching and animal foraging shaped interaction frequencies between plants and birds in frugivory networks. The generality of trait matching is the base for predicting unknown interactions from species' functional traits in novel ecological communities (Kissling and Schleuning 2015), for instance as a result of species' migrations and local extinctions in response to climate change. Furthermore, we show that the degree of functional specialization of plants and birds is weakly, but significantly associated with specific morphological traits. The identification of these traits is useful for the identification of plant and bird species that fulfill functionally specialized roles in current and future communities.

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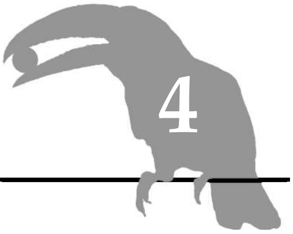
SUPPLEMENTARY MATERIALS

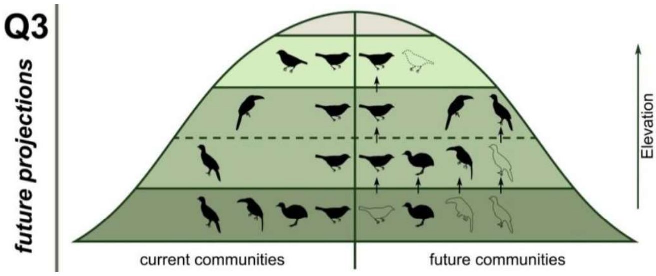
The following supplementary materials are available from pp. 117–132:

Supplement 3.1	Sampling of the interaction networks.
Table S3.1	Comparison between the meta-analyses weighted by sampling effort and sampling completeness.
Figure S3.1	Accumulation curves and asymptotic bird richness for the eight interaction networks across the Andes.
Figure S3.2	Accumulation curves and asymptotic link richness (*i.e.*, the number of interacting species pairs) for the eight interaction networks across the Andes.
Figure S3.3	Fourth-corner correlations between functional traits of frugivorous bird species and fleshy-fruited plant species across the Andes.



Chapter 4

Effects of climate change on functional diversity of birds on a tropical mountain



Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Nowak, L., Töpfer, T., Wiegand, T., Dehling, D.M. and Schleuning, M.

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EFFECTS OF CLIMATE CHANGE ON FUNCTIONAL DIVERSITY OF BIRDS ON A TROPICAL MOUNTAIN

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SUMMARY

Climate change forces species to move their ranges upwards. Resulting changes in community composition might lead to losses in functional diversity (FD). We combined approaches from biogeography (species distribution models; SDMs) and community ecology (FD) to investigate potential effects of climate change on frugivorous bird communities along a 3000 m elevational gradient in the tropical Andes. We modeled current and projected future occurrence probabilities of bird species from the lowlands up to the treeline and combined them with functional traits relevant for seed dispersal into FD calculations. Comparisons of functional richness (unweighted) and functional dispersion (weighted by probabilities of occurrence) between current and projected future communities showed consistent signals of functional attrition in the lowlands, an unexpected increase of FD at lower mid-elevations and no consistent support for functional decrease at high elevations. These projections reveal that FD responds differently to climate change at different elevational levels along tropical mountains.

INTRODUCTION

Climate change is one of the main threats to biodiversity and its intensity is expected to increase in the future (Agard *et al.* 2012). Species in tropical ecosystems are particularly sensitive to climate change, due to low climatic variability and high niche specialization of species (Janzen 1967, McCain 2009). Climate change might be especially relevant in tropical mountains because of their high rate of species turnover (Dehling *et al.* 2014a) and steep temperature gradients, while latitudinal temperature gradients in the tropics are shallow (Colwell *et al.* 2008). In response to changing climate, species are expected to maintain their preferred climatic niche by altering their geographical and elevational ranges (Parmesan and Yohe 2003, Colwell *et al.* 2008). In mountainous areas, species are therefore likely to shift their distribution upwards in response to increasing temperatures (Colwell *et al.* 2008), leading to changes in biodiversity composition along elevational gradients (Parmesan 2006). Vertical range changes have already been observed for a variety of taxa, including insects, vertebrates and plants (Pounds *et al.* 2005, Chen *et al.* 2009, Feeley *et al.* 2011, Freeman and Class Freeman 2014). However, there is a lack of knowledge on how diversity patterns might change under climate change on highly diverse tropical mountains.

Changes in biodiversity along elevational ranges might occur in a variety of ways (Colwell *et al.* 2008). When species at a given elevation move their elevational ranges upwards in response to increasing temperatures, species from lower elevations that are already adapted to higher temperatures could move in and replace the emigrating species (Colwell *et al.* 2008). These range shifts might cause species turnover that could buffer changes in species richness at different elevations on a mountain. There are, however, two exceptions. At the lowest elevations, upward range shifts and a lack of compensation by immigrating species might lead to a net loss of species richness in the tropical lowlands, a process referred to as "biotic attrition" (Colwell *et al.* 2008, Feeley and Silman 2010b). At the highest elevations, species face a different challenge since they are not able to move their ranges beyond the mountaintop. This could lead to mountaintop extinctions and the loss of specific species from the community (Peters and Darling 1985, Colwell *et al.* 2008). In addition, other physical or biotic barriers could limit upward movements of species on mountains and cause local extinctions of species, for instance at the treeline of tropical mountains (Rehm and Feeley 2016). Beyond these general theoretical expectations, very little is known about compositional and functional changes of ecological communities along mountains in response to climate change.

Taxonomic measures of biodiversity, such as species richness, are insufficient to describe the functional relevance of biodiversity (Tilman 2001). When knowledge is available about which traits relate to a specific ecosystem function (Violle *et al.* 2007), the range and distribution of these functional traits, *i.e.*, their functional diversity (FD), can describe how an ecological community contributes to ecosystem functioning (Tilman 2001). A variety of complementary metrics are available to quantify FD (Villéger *et al.* 2008, Mouillot *et al.* 2013). One way is assessing the amount of potential functional roles that a community fulfills by quantifying the volume of the overall multidimensional functional trait space (functional richness, FRic, Villéger *et al.* 2008). Another way is to measure the average dissimilarity among species which is related to the potential for functional complementarity among species (functional dispersion, FDis, Laliberté and Legendre 2010). While most research on FD has focused on local communities, there is now also increasing interest to study FD at biogeographic scales (Violle *et al.* 2014). This approach can provide insights into the geographic distribution of functional trait diversity across latitudinal and elevational gradients (*e.g.*, Dehling *et al.* 2014a, Barnagaud *et al.* 2017). The combination of species distribution models (SDMs) with future climate change scenarios and FD analyses (Barbet-Massin and Jetz 2015) is a promising approach to studying climate change impacts on FD (Violle *et al.* 2014, Kissling and Schleuning 2015). Applications of this approach to species-rich elevational gradients in the tropics are lacking to date, since accurate data on species distributions, local community composition and functional traits are difficult to obtain, especially for tropical mountains.

Here we combine SDMs with FD analysis to study the potential effects of future climate change on frugivorous bird communities along the forested part of an elevational gradient in the Manú Biosphere Reserve in the Peruvian Andes (studied range, at 500 m steps: 500–3500 m a.s.l., Fig. 4.1). We focus on frugivorous birds because they are of key importance for the

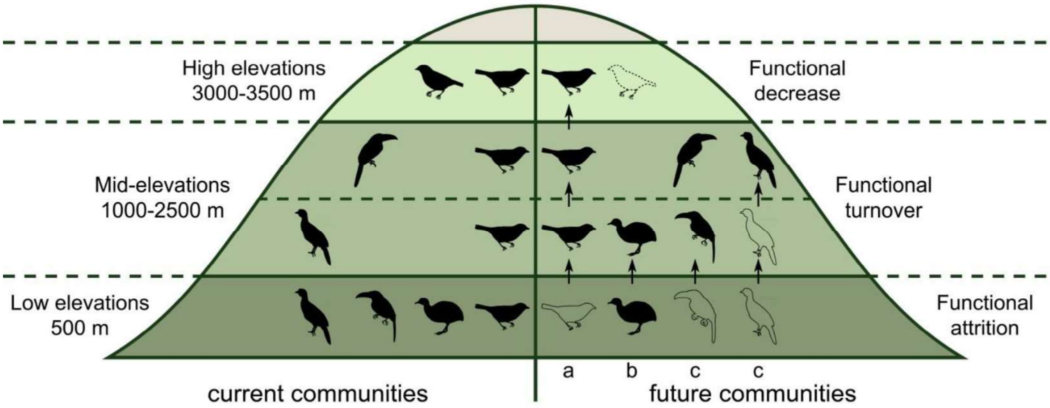


Figure 4.1. Current and potential future patterns in functional diversity (FD) of frugivorous bird communities along an elevational gradient in the Peruvian Andes. Current patterns in bird diversity are shown on the left ("current communities") and expected changes under future climate change are shown on the right side of the mountain ("future communities"). Currently, low elevations harbor the highest FD, and FD decreases with increasing elevation. In the future, projected changes could include (i) losses of FD at the lowest elevations (functional attrition), (ii) a rather constant FD at mid-elevations (functional turnover) if species immigration and emigration are functionally balanced, and (iii) species-level losses at high elevations (functional decrease), due to a dispersal barrier beyond the treeline. Ranges of species can either contract (a), expand (b) or shift (c) in response to projected climate change; black bird silhouettes indicate the presence of a species on an elevational level, species outlines indicate that a species moved out of the respective elevational level, and the dotted silhouette indicates species extinction from the entire mountain. The entire gradient covers an elevational range from the lowland (250 m) up to the mountaintop (3750 m). Forests cover the mountain up to 3500 m (green shading) and the studied gradient covers 500–3500 m of elevation.

functioning of tropical forest, due their important role as seed dispersers (Herrera 2002, Kissling *et al.* 2009). Their functional role as seed dispersers can be described by morphological traits related to fruit handling and swallowing, flight performance, bipedal locomotion and body mass (Dehling *et al.* 2014a). By modeling current and future occurrence probabilities of bird species at different elevations, and integrating them with seed dispersal relevant traits into FD calculations, we explore how future climate change might affect FD of bird communities along this tropical elevational gradient. Future projections of current communities were derived via two steps. First, we projected species' elevational ranges according to future temperature scenarios (WorldClim, Hijmans *et al.* 2005) and tropospheric lapse-rates (Mokhov and Akperov 2006) for three dispersal scenarios that assume that birds need to move upwards to track their temperature niche (Fig. 4.2a). These scenarios include: *range contraction* (upwards shift of lower range limit), *range expansion* (upwards shift of upper range limit) and *range shift* (upwards shift of both lower and upper range limit). Second, we used SDMs based on mean annual temperature (MAT) and mean annual precipitation (MAP) to model current and future occurrence probabilities of bird species on each of the seven studied elevational levels. To assess possible changes in FD under climate change, we calculated FRic (unweighted) and FDis (weighted by SDM derived occurrence probabilities) for current and projected future communities.

We hypothesized (Fig. 4.1) that climate change will lead to (i) a loss of FD on the lowest elevation of the gradient (due to functional attrition), (ii) little change in FD at mid-elevations if the loss of emigrating species is compensated by immigration of functionally similar species (functional turnover), and (iii) a reduction in FD due to loss of species at high elevations (functional decrease) since frugivorous bird species are not able to move past the current treeline. It remains unclear, however, to what extent this decrease could be functionally compensated by immigration of species from mid-elevations.

RESULTS

A total of 245 frugivorous bird species currently occur along the elevational gradient of the Manú biosphere reserve, of which 240 species could be included in this study (Table S4.1). The highest number of species was found on the lowest elevational level (*n* = 146 at 500 m a.s.l., hereafter ‘m’), followed by a continuous decrease of species richness towards higher elevations (*n* = 19 at 3500 m). None of the breeding species occurred on all elevational levels. 62 species were restricted to the lowlands (≤ 500 m) of which seven only occurred below 500 m. Five species were restricted to the highlands (3000–3500 m). Our dataset included both species that are widely distributed across South America (*e.g.*, the parrot *Aratinga leucophthalma* with 2308 GBIF occurrence records across South America) and narrowly distributed species (*e.g.*, the barbet *Eubucco tucinkae* with 86 GBIF occurrence records). The species pool covered a wide range of trait values, *e.g.*, body mass ranged from 7.2 g (the tyrannulet *Zimmerius gracilipes*) to 2813 g (the curassow *Mitu tuberosum*).

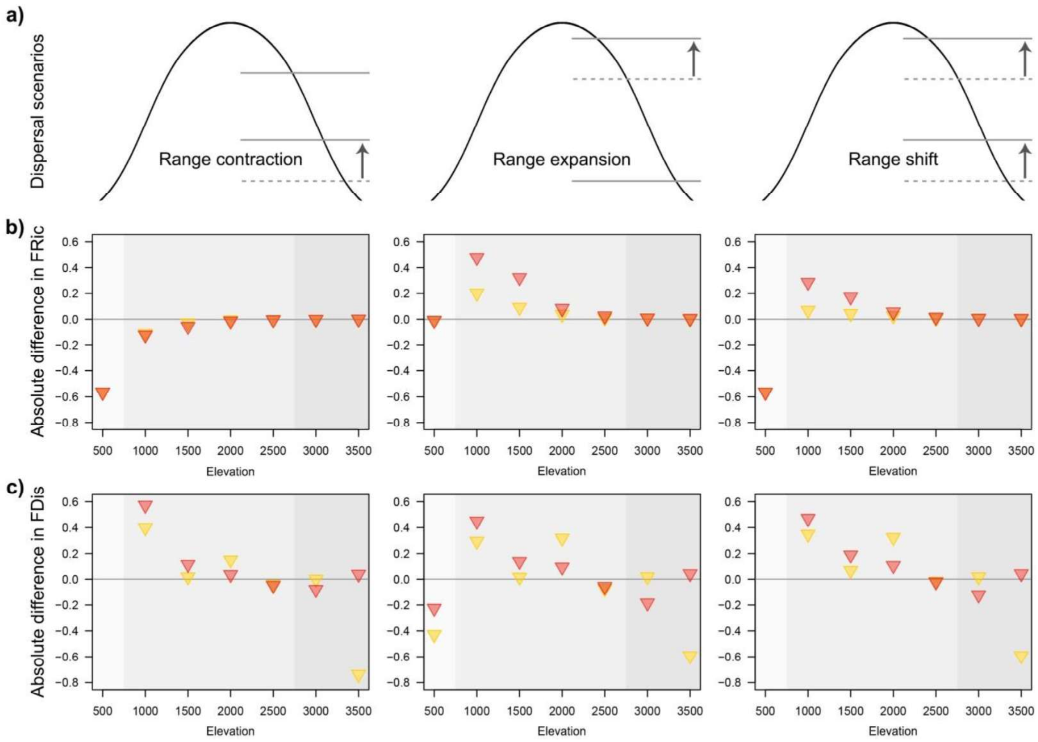
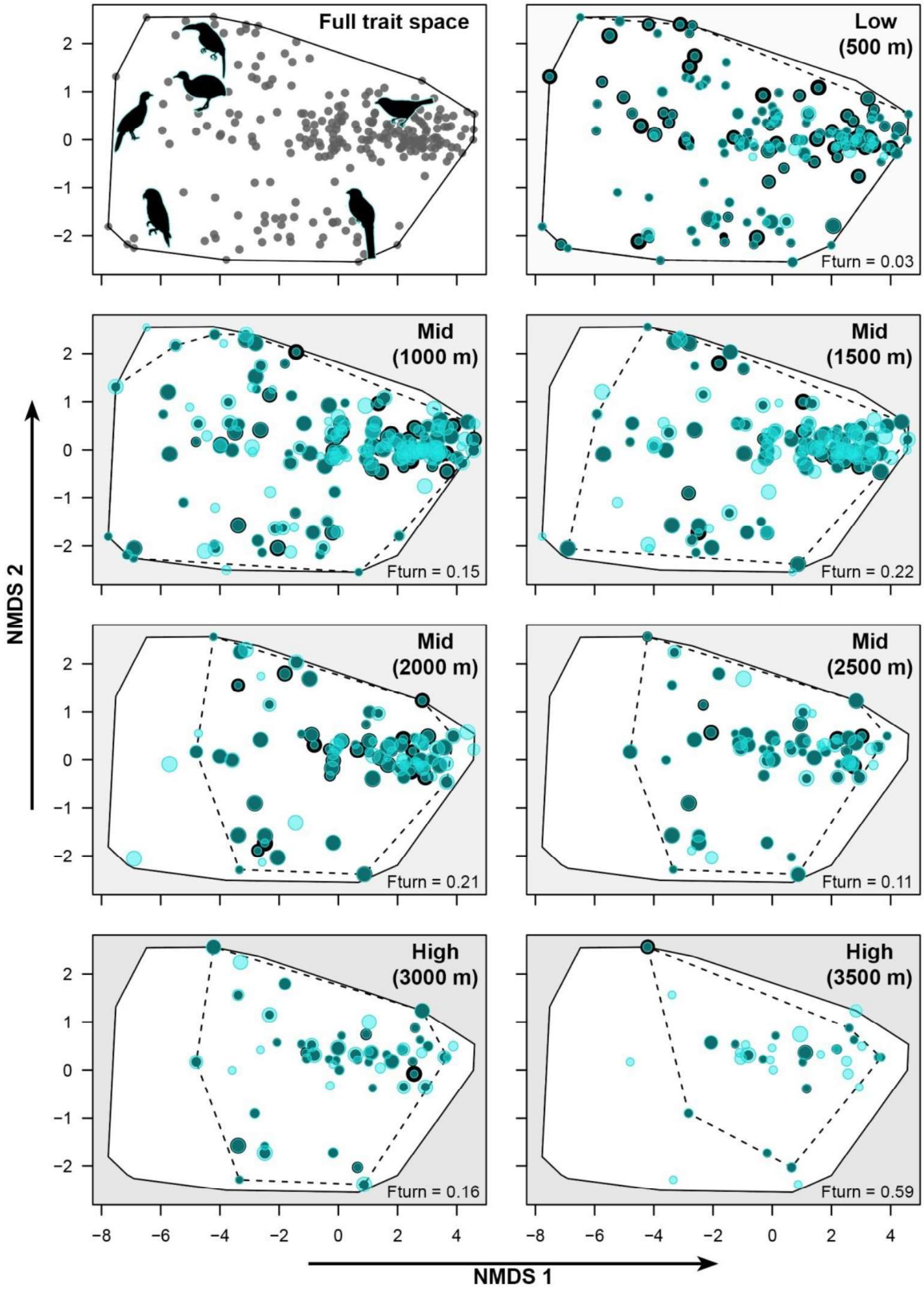


Figure 4.2. Dispersal scenarios and their consequences for functional diversity (FD) of bird communities under projected future climate change. (a) Three potential dispersal scenarios representing *range contraction* (lower range limit moves upwards), *range expansion* (upper range limit moves upwards), and *range shift* (both lower and upper range limit move upwards). (b, c) Projected changes in functional richness (FRic) and functional dispersion (FDis) of bird communities for each of seven elevational levels, representing a gradient from 500 m to 3500 m (at 500 m steps). Absolute changes in FD are based on species distribution models (SDMs) of 240 birds under current and projected future climate change scenarios using two representative concentration pathways: RCP 6.0 (yellow) and RCP 8.5 (red). FD (FRic and FDis) calculations were derived using ten morphological bird traits and are based on presence/absence of birds (FRic) or their SDM-derived probability of occurrence (FDis). Positive FRic and FDis values indicate an increase of FD under climate change, and negative values a decrease. Missing symbols for an elevational level indicate that no species occurred at this elevation in the projected future.

SDMs performed generally well (prediction accuracy across all SDMs measured as true skill statistic, mean TSS = 0.87 ± 0.07). Overall, mean annual temperature (MAT) was projected to increase considerably along the elevational gradient under both considered representative concentration pathways (RCP, from the Fifth Assessment Report of the IPCC, Hijmans *et al.* 2005, Flato *et al.* 2013), *i.e.*, RCP 6.0 ($\Delta T = 2.3 \pm 0.06$ °C) and RCP 8.5 ($\Delta T = 3.3 \pm 0.08$ °C). The mean vertical distance a species had to move to track its preferred temperature niche, according to our projections, ranged between 360 m and 400 m under RCP 6.0 and between 520 m and 580 m under RCP 8.5. Based on these projections, we calculated functional richness (FRic, unweighted) and functional dispersion (FDis, weighted by SDM derived occurrence probabilities) of projected future bird communities and compared these to estimates from current communities. We compared projected changes in FRic and FDis for all three dispersal scenarios (*range contraction*, *expansion* and *shift*; Fig. 4.2a).

In line with the first expectation, we generally found strong support for functional attrition, *i.e.*, the loss of FD in the lowlands (at 500 m) (Fig. 4.2). This was consistent across FD metrics (FRic and FDis), dispersal scenarios (especially *range contraction* and *range shift*) and



both emission scenarios (RCP 6.0 and RCP 8.5) (Fig. 4.2, Figs. S4.1–S4.5, 500 m). Under the *range expansion scenario*, functional attrition was not observed for FRic (Fig. 4.2b, middle). However, it was still evident for FDis (Fig. 4.2c, middle) which can be explained by a decrease in occurrence probabilities of species at the margins of the functional trait space (Fig. 4.3 and S4.3, 500 m).

Regarding the second expectation, we hypothesized that functional turnover of species would lead to little change in FD at mid-elevations of the gradient. Our results confirmed this at the higher mid-elevation (2500 m) where there was little to no projected change in FRic and FDis, regardless of the dispersal scenario (Fig. 4.2b, c). At this elevational level, species with projected increasing occurrence probabilities had similar relative positions in functional trait space as species with projected decreasing occurrence probabilities, leading to little functional turnover between current and projected future communities (Fig. 4.3, 2500 m). At the lower mid-elevations (1000–2000 m), we mostly found an increase in FRic and FDis (Fig. 4.2b, c), contrary to our expectation. At these elevations, probabilities of occurrence of species at the margins of the functional trait space tended to increase, while probabilities of occurrence decreased mainly in the center of the trait space (Fig. 4.3, 1000–2000 m). Functional turnover between current and projected future communities was consistently higher at these elevational levels than at 2500 m (Fig. 4.3, Figs. S4.1–S4.5). These results suggest an increase of FD at lower mid-elevations, due to an increase of functionally specialized species and a high functional turnover between current and future communities at these elevations.

Finally, we hypothesized that a loss of species could lead to a decrease of FD at the highest elevation. We found little support for this hypothesis because the models did neither project species extinctions nor a consistent decrease of FD in the highland communities (Fig.

Figure 4.3. Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range expansion scenario*. The functional trait space is derived from Nonmetric Multidimensional Scaling (NMDS, based on Euclidean distances) which condenses the dissimilarity of ten morphological bird traits (bill width, bill length, bill height, tail length, tarsus length, tarsus sagittal width, tarsus lateral width, wing length, Kipp's distance and body mass) onto two axes (NMDS 1, NMDS 2). Trait spaces are shown for the entire bird community (upper left) and for communities on each of the seven elevational levels (500 m to 3500 m, at 500 m steps). Black polygons illustrate the functional trait space of the entire bird community. Black stippled polygons illustrate the functional trait space of the current local community at the given elevation. Each dot represents one bird species (n = 240). Within each elevational level, dot size represents the probability of occurrence as derived from SDMs. Black dots represent current communities, transparent green dots represent occurrence probabilities under projected climate change (based on the RCP 6.0 scenario for 2070, MIROC5 climate model). Species-level changes are visible in four ways: (1) complete black dots indicate future loss of species, (2) complete green dots indicate future immigration of species, (3) dark green dots with a black ring indicate future decline in occurrence probability, and (4) dark green dots with a light green ring indicate future increase in occurrence probability. Functional turnover (Fturn) between current and projected future communities is provided in the bottom-right corner of each trait space (see Methods for details). Bird silhouettes in the upper left panel indicate the approximate location of key taxonomic groups in trait space (counterclockwise from top): toucans, tinamous, guans, parrots, trogons and tanagers.

4.3, 3000–3500 m). While FRic was generally similar between current and future communities at 3000–3500 m elevation (the upper end of the forest on the mountain; Fig. 4.2b), there was substantial variation between the two emission scenarios for FDis values (Fig. 4.2c) and high functional turnover between current and projected future communities under most dispersal scenarios (Fig. 4.3, Figs. S4.1–S4.5). Together, this indicates a high potential for functional changes at these elevations, but also a large uncertainty in projected future FDis.

DISCUSSION

We combined SDMs with FD analysis to explore how climate change might affect the FD of frugivorous bird communities along an elevational gradient in the Andes. Comparisons between current and projected future frugivore communities provided insights into the potential future changes in FD. We found strong support for functional attrition in the lowlands, an increase of FD at lower mid-elevations and little change in FD at elevations above 2500 m. These findings suggest that climate change might have various effects on biodiversity and ecosystem functioning along tropical mountains.

Models consistently predicted large losses of FD of frugivore communities in the lowlands. These losses were found in all scenarios (two FD metrics, three dispersal scenarios and two RCP scenarios), underlining that functional attrition would be a major risk for future lowland frugivore communities. The loss of FD indicates that functionally specialized species (with a set of morphological traits that are different from the rest of the community) might decrease in prevalence in the future. These functionally specialized species provide complementary functions to the community and their loss is expected to lead to a loss of seed dispersal functions in the lowlands, especially for plant species with extreme morphologies, such as large-fruited plants (Levey 1987, Dehling *et al.* 2016). Species that were projected to be lost from future lowland bird communities included, for instance, the functionally specialized razor-billed curassow (*Mitu tuberosum*), or the chestnut-eared and ivory-billed aracari (*Pteroglossus castanotis*, *P. azara*). Non-random loss of functionally specialized species already happens in response to land-use change (Flynn *et al.* 2009), *e.g.*, large-bodied frugivores are particularly affected by habitat disturbance (Bregman *et al.* 2016) and hunting (Peres and Palacios 2007). Here we show that similar effects on functionally specialized species could be expected as a consequence of climate change in tropical lowlands. This is especially alarming since the effects of human land use on bird diversity are also most severe at the base of tropical mountains (Ferger *et al.* 2017).

In contrast to losses in the lowlands, the models predicted an unexpected increase of FD at the lower mid-elevations (1000–2000 m) of the gradient. This suggests that there is a high potential for species immigration at the margins of the functional trait space at these elevations. The major factor driving this trend is the projected upwards dispersal of many lowland species in response to climate change (Parmesan 2006, Feeley and Silman 2010). This potentially causes the immigration of functionally specialized species to the lower mid-elevations, such as the oilbird (*Steatornis caripensis*) or the white-throated toucan (*Ramphastos tucanus*). The immigration of such species is likely to cause a high functional turnover between current and projected future communities at these elevations. Another factor is the increase in occurrence probability of species with specialized morphologies that were already present in the current communities. The razor-billed curassow (*Mitu tuberosum*) and ivory-billed aracari (*Pteroglossus azara*) were currently present at the mid-elevation, but were projected to have increasing probabilities of occurrence under projected future climate.

A high species turnover between bird communities at mid elevations has been observed previously on tropical mountains (*e.g.*, Jankowski *et al.* 2013, Dehling *et al.* 2014a). The occurrence of different species with similar functional traits at different elevations could foster functional redundancy among species on the Manú gradient. This could be an important mechanism in maintaining ecosystem functions, such as seed dispersal, as the immigration of species with similar or new functional traits could compensate for the loss of other species (Pigot *et al.* 2016, Bender *et al.* 2017). However, the immigration of species could be limited by competition with persisting, functionally similar species in these communities (MacArthur and Levins 1967, Fleming 1979). Moreover, the potential of a novel community to rewire species interactions, such as those between plants and birds, is not yet understood and would be essential for maintaining ecosystem functioning at these elevations (Schleuning *et al.* 2016, Bender *et al.* 2017). Despite the projected species turnover and a high potential for functional compensation, it is not yet clear how mid-elevation communities and their associated interaction networks will re-assemble in the future.

At the highest elevations close to the Manú treeline, we expected a loss of species from the communities, but all species currently present in the community were projected to persist. This could be a consequence of the width of the elevational ranges of species at these elevations. According to Rapoport's rule (Stevens 1989, 1992), species in the lowlands tend to have narrow elevational ranges, whereas species at high elevations tend to have wide elevational ranges, covering several elevational levels. This pattern potentially mitigates functional decreases at high elevations since highland species might have wide elevational ranges and therefore potentially broad climatic niches, which would make them rather robust to future climate change. The blue-and-yellow tanager (*Thraupis bonariensis*), for example, occurs from 1000–3500 m and the band-tailed pigeon (*Patagioenas fasciata*) from 1500–3500 m, while their projected range shift was 370 m and 520 m under RCP 6.0 and RCP 8.5, respectively.

At the community level, we found an important discrepancy between the FDis results under the RCP 6.0 and RCP 8.5 scenario. This indicates a large uncertainty in the assessment of future FD at high elevations. Current FD is small in high-elevation communities as a consequence of environmental filtering, as only species with certain combinations of traits can persist under harsh environmental conditions (Webb *et al.* 2002, Dehling *et al.* 2014a). At these elevations, the functional trait space is only sparsely filled and functional redundancy is low. Consequently, the increase or decrease in the probability of occurrence of a single species can have a huge impact on the FD of these communities, which is also reflected by a high potential for functional turnover. For example, the 25% decline in occurrence probability of the morphologically specialized grey-breasted mountain toucan (*Andigena hypoglauca*) under projected future climates would hugely affect FDis. The highest elevation on our gradient (3500 m) coincides with the tropical treeline. Here, forest ecosystems reach their upper limit and the highland grasslands hinder upwards shifts of the forests (Rehm and Feeley 2015), which might constrain bird movements to higher elevations (Rehm and Feeley 2016). Little functional redundancy and idiosyncratic changes in the FD of bird communities may, thus, lead to unpredictable community dynamics at the treeline.

Overall, model projections suggested that FD of frugivorous birds is expected to change substantially, which would lead to distinct changes of FD at different elevational levels. Other factors than climate might additionally influence bird community composition (Dehling *et al.* 2014a) and constrain species movement along elevational gradients. For instance, topographical differences between lowland and montane forests were not considered in the present study, but could hinder the upward movement of species, such as ground-dwelling birds, in response to climate change (Dehling *et al.* 2014a). Elevation-specific community changes of frugivorous birds could have an important feedback on ecosystem functioning because birds are an essential asset for plant regeneration processes (Howe and Smallwood 1982, Markl *et al.* 2012, Rodríguez-Pérez *et al.* 2012). For example, the loss of frugivores with long, pointed wings, such as macaws (*Ara* spp.), could lead to the loss of long-distance seed dispersal that is required to maintain forest connectivity (Müller *et al.* 2014) and colonization potential (Howe and Smallwood 1982). In addition, frugivorous birds and fleshy-fruited plants could respond differently to climate change (Parmesan 2006), which could lead to functional mismatches between the two groups. Since bird distributions are directly related to plant distributions along tropical mountains (Jankowski *et al.* 2013, Dehling *et al.* 2014b), upslope movement of birds could be slowed down if the plant community responds more slowly to climate change.

In conclusion, we show that the combination of SDMs and FD is a promising way to study the potential functional changes in ecological communities under future climate change. In particular, studies that examine the effects of climate change on tropical mountains yield unique insights into the manifold potential responses of ecological communities to future changes. Our study reveals how bird communities at different elevations of a tropical mountain could be affected differently by projected future changes. On the one hand, lowland communities are likely to face a loss of ecological functionality in the future. On the other hand, communities at mid-elevations are likely to reshuffle in the future, which poses high pressures on these communities to adapt to changes in community composition.

METHODS

Bird data

Current elevational ranges of the 245 frugivorous bird species in the Manú biosphere reserve (Andes of south-eastern Peru, 250–3750 m) were obtained from Dehling *et al.* (2014a), who combined the data (derived from bird observations via sight, sound or sign records) from Walker *et al.* (2006) and Merkord (2010), complemented with data collected by D.M. Dehling during field work in Manú between December 2009 and September 2011. We used these local elevational distribution ranges of birds to derive local community composition at seven elevational levels of the elevational gradient in the Manú biosphere reserve (500–3500 m, at 500 m steps).

We additionally downloaded occurrence records for each bird species from the global biodiversity information facility (GBIF; www.gbif.org) to be used to fit the species-specific SDMs. The data was subjected to a comprehensive quality check, in which we deleted all entries without coordinates, with coordinates located outside the extent of South America (81.5° W to 34.5° W, 56° S to 12.5° N), and all entries where coordinates and country of origin did not match. This resulted in a total of 16–9,138 occurrence records per species. Species with less than 40 occurrence records were considered unsuitable for modelling and were consequently excluded from further analysis. This resulted in a species pool of 240 frugivorous bird species with 46–9,138 occurrence records (mean = 1096, SD = 1140) per species.

To quantify FD, we measured ten morphological traits which quantify species' characteristics that are relevant for seed dispersal by frugivorous birds (Dehling *et al.* 2014a). Traits related to beak morphology influence seed dispersal by imposing direct constraints on the possibility that a bird is able to handle and swallow a fruit (Wheelwright 1985, Stang *et al.* 2009, Dehling *et al.* 2014b). Traits related to flight performance and bipedal locomotion influence which fruits a foraging bird species encounters (Moermond and Denslow 1985, Schleuning *et al.* 2011). Finally, body mass (g) gives an indication of the energy requirements of a bird and therefore the type of fruits it might prefer (Belovsky 1997, Petchey *et al.* 2008). All traits were measured on at least four museum specimens for each of the 240 bird species, mainly following Eck *et al.* (2011). Specifically, the ten traits included bill width, length and height (mm), tail length (mm), tarsus length and tarsus sagittal/lateral width (mm), wing length (mm), Kipp's distance (the distance between the tip of the first secondary and the wing tip, measured on the folded wing, in mm), and body mass (g).

Climate

Climatic data on mean annual temperature (MAT) and mean annual precipitation (MAP) were compiled across South America (for fitting continental SDMs) and at the local level along the elevational gradient of the Manú biosphere reserve (for local SDM projections). Local mean annual temperature (MAT) and mean annual precipitation (MAP) for each of the seven elevational levels were compiled from literature (Girardin *et al.* 2010, Girardin *et al.* 2013) and from local measurements by W. Farfan-Rios (elevation 3500 m) and C. Beirne (CREES, MLC, elevation 500 m). The use of local MAT and MAP data was preferred over the use of global climate data since they were measured on site and therefore were not affected by interpolation between climate stations in mountainous areas.

To compile the future climate projections for the seven elevational levels, we downloaded current and future projected climate rasters for MAT and MAP from WorldClim (Hijmans *et al.* 2005) at a spatial resolution of 2.5 minutes (approx. 4.6 km on the equator). Current climate values from WorldClim are based on a 20 year time period between 1960–1990 ("current") and the future projected climate values on the 20 year time period between 2061–2080 ("2070"). Future climate projections were downloaded for a general circulation model from the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (MIROC5, Hijmans *et al.* 2005, Flato *et al.* 2013), using two representative concentration pathways (RCP), RCP 6.0 (assumed global average increase of 2.85 ± 0.62 °C in MAT) and RCP 8.5 (assumed global average increase of 4.02 ± 0.80 °C in MAT). We compared these projections to those from another climate model (CCSM4, Hijmans *et al.* 2005, Flato *et al.* 2013), which resulted in qualitatively identical results. Projected climate anomalies were calculated by subtracting the current MAT and MAP rasters from the projected future MAT and MAP rasters. For the local gradient, we extracted the MAT and MAP anomaly values from the locations of the seven studied elevational levels (in seven grid cells of 2.5 minutes resolution) in which the Manú elevation gradient was located. Anomalies were added to the respective local MAT and MAP values to obtain the future projected climate along the local Manú elevational gradient.

Bird communities

We assembled current bird communities for each elevational level along the Manú elevational gradient using the current elevational range data of birds (see above and Table S4.1). A species was considered to be present in a community of an elevational level when that elevation fell within the elevational range of a species. This resulted in a binary presence/absence matrix of the 240 bird species at the seven elevational levels (500–3500 m, at 500 m steps). Future bird communities were assembled by projecting potential future elevational ranges of birds (based on our climate projections along the gradient; see below) in order to construct a binary matrix of the 240 bird species at the seven elevational levels (500–3500 m, at 500 m steps). This procedure was repeated for each of the three dispersal scenarios (*range contraction*, *expansion*, and *shift*) and two RCP scenarios (RCP 6.0, RCP 8.5), leading to six potential future bird communities per elevational level.

To project future elevational ranges, we acquired annual mean tropospheric lapse-rate values (*i.e.*, how temperature decreases with an increase in altitude) at a resolution of 2.5° (approx. 276 km at the equator) for the period 1948–2001 from Mokhov and Akperov (2006).

This lapse-rate raster was bilinearly interpolated to match the resolution of 2.5 minutes of the mean annual temperature (MAT) rasters and ranged between 6.17 °C/km and 6.22 °C/km. Following La Sorte and Jetz (2010), we then estimated the projected vertical shifts in temperature by dividing the projected temperature anomaly (°C) by the cell's tropospheric lapse rate (°C/km). Projected vertical distances (km) were extracted for the entire Manú elevational gradient, *i.e.*, for the locations of the seven studied elevational levels (seven grid cells) and two additional grid cells which represent the lowest (250 m) and highest (3750 m) point of the Manú elevational gradient (all grid cells at a 2.5 minutes resolution). For species which occur on X elevational levels, we therefore calculated X projected vertical distance values, which were averaged to obtain a species-specific vertical distance shift. The mean projected vertical distance per bird species was calculated in this way for both future 2070 emission scenarios (RCP 6.0 and RCP 8.5).

The future elevational range of each species was subsequently calculated by adding the mean projected vertical distance per species to the lower and/or upper values of their elevational range, depending on the respective dispersal scenario (see Table S4.1 for current and projected future elevational ranges of all bird species). We projected the future elevational ranges with three different dispersal scenarios under the assumption that species have to move upwards to track their climate niche (Chen *et al.* 2011). First, under the *range contraction scenario*, bird species could only have an upslope movement of their current lower range limit, while the upper limit remained constant. This leads to a contraction of species ranges (Fig. 4.2a left). Second, under the *range expansion scenario*, bird species were projected to expand their range upwards, while the lower limit of their elevational range remained the same (Fig. 4.2a middle). Third, under the *range shift scenario*, bird species could move their complete range upwards, *i.e.*, both the lower and upper limit changed (Fig. 4.3a right).

Species distribution models (SDM)

We used species distribution models (SDMs) to obtain the current and projected future probability of occurrence of the 240 bird species within each of the seven elevational levels of the Manú biosphere reserve. All SDMs were fitted on a spatial extent of continental South America to capture the whole climatic niche space of each species. Since spatial sampling bias (*e.g.*, towards easily accessible areas or due to differences in sampling intensity among taxa) can affect the performance of SDMs, we minimized its effect by following the suggestions from Phillips *et al.* (2009) by restricting the background data to an extent with the same spatial bias as the pooled data of all species occurrences. Thereto, we downloaded GBIF occurrence records for all bird species in South America and restricted the background to only those grid cells in which at least one bird species was observed. This resulted in a background of 34,297 grid cells (2.5 minutes resolution) across the entire extent of continental South America.

To identify the best performing model for each bird species, we compared five SDM methods: generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (GBM), random forest (RF) and maximum entropy models (MAXENT) (Thuiller *et al.* 2014). SDMs were based on mean annual temperature and precipitation values (WorldClim, Hijmans *et al.* 2005). As a random cross-validation of model performance, species occurrence data were split into 80% calibration data and 20% evaluation data. Prior to model fitting, we selected pseudo-absence (PA) records following the suggestions of Barbet-Massin *et al.* (2012). We selected 10,000 random PAs from the background data for fitting GLM and GAM models. For the GBM and RF models, we selected the same amount of PAs as there were presence data (occurrence records) available for each species. For these two methods, we ran the models ten times per species, each run with a new selection of PAs. Only the best of the ten models was then considered further. For MAXENT, the presence records were contrasted against the entire background because presence/absence is not measured (Phillips and Dudík 2008). All SDMs were evaluated with the true skill statistic (TSS) evaluation metric, *i.e.*, the sum of sensitivity and specificity minus one (the sensitivity is the proportion of correctly predicted presences, and the specificity is the proportion of correctly predicted absences). The cut-off value of the models, *i.e.*, the threshold value of the probability of occurrence that maximizes the TSS metric for each model, ranged between 0.30–0.95 (see Table S4.3). The often used area under the curve of the relative operating characteristic, AUC/ROC, is known to be flawed (*e.g.*, Jiménez-Valverde *et al.* 2008, Lobo *et al.* 2008) and was therefore not used in this study. To decide which of the five modeling methods performed best for the respective species, we selected that with maximum TSS (see Table S4.3 for model evaluation metrics for all SDMs).

The best performing SDM was used to determine the probability that a species could occur on each of the seven elevational levels. To do this, we projected the SDMs using the current local climate (BIOMOD_Projection in "biomod2" package in R, Thuiller *et al.* 2014) as well as the two future local climates (2070; RCP 6.0 and RCP 8.5). These SDM-derived probabilities of occurrence were multiplied with the binary community matrix of the 240 bird species on the seven elevational levels (see Table S4.2 for current and future probabilities of occurrence of all bird species). Hence, if a species was not present at an elevational level according to its elevational range, it remained absent; if a species was present, the value of 1 was substituted by the probability of occurrence derived from the SDM.

Functional diversity of bird communities

For all current and future communities, according to the three different dispersal scenarios (*range contraction*, *expansion* and *shift* under RCP 6.0 and RCP 8.5), we calculated two FD metrics: functional richness (FRic) and functional dispersion (FDis). The two metrics describe two complementary aspects of FD. FRic measures the proportion of functional space filled by species in the respective community (Mason *et al.* 2005), whereas FDis quantifies the weighted average distance of all species to the weighted centroid of a community (Laliberté and Legendre 2010). Hence, FRic is independent of species' probabilities of occurrence, whereas FDis uses a weight for each species, based on the probability of occurrence of each species in current and projected future communities. We calculated functional diversity metrics with the dbFD function in the "FD" package in R (Laliberté *et al.* 2014), based on the ten log-transformed morphological bird traits (see above). Dissimilarities between species were calculated based on the Euclidean distance between species. These dissimilarities were used to project the variability in the ten morphological traits onto ten axes in a Principle Coordinate Analysis (PCoA). FRic and FDis values were calculated from the resulting ten-dimensional trait space. FRic and FDis values were compared between current and projected future communities to determine the effect that climate change might have on the FD of bird communities along the elevational gradient.

In addition to FRic and FDis, we estimated the functional turnover between current and projected future communities by calculating the mean Euclidean distances in functional trait space from all species in one community to their functionally most similar species in the other community (Dehling *et al.* 2014a). For a species that is present in the current and the respective future community, this distance is zero. Hence, large values of functional turnover indicate that changes in community composition lead to the emigration or immigration of functionally distinct species, whereas small values indicate turnover of species with similar traits.

To reduce the dimensionality and to visualize the functional trait spaces of current and projected future bird communities (see Fig. 4.3), we computed the Euclidean distances between species in PCoA space and used these distances in a Nonmetric Multidimensional Scaling (NMDS, metaMDS in "vegan" package in R). The NMDS condensed the variation of the ten PCoA axes onto two axes. The scaling achieved a stable solution (stress value = 0.07) and the two NMDS dimensions can therefore be considered representative for visualizing the overall trait variation among species based on the ten morphological traits.

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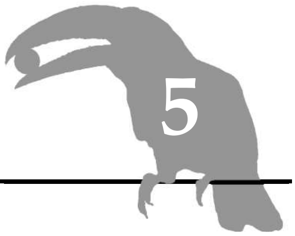
AUTHORS' CONTRIBUTIONS

All authors were involved in conceiving the general ideas. I.M.A.B., W.D.K., D.M.D. and M.S. conceived and designed the study. D.M.D., I.M.A.B and T.T. collected the data. I.M.A.B. performed the analysis with input from W.D.K. and M.S. All authors discussed the results. I.M.A.B. wrote the first draft of the manuscript with input from W.D.K. and M.S. All authors commented on the manuscript and approved the final version of the manuscript.

SUPPLEMENTARY MATERIALS

The following supplementary materials are available from pp. 133–161:

Table S4.1	Current and future elevational ranges of all 240 frugivorous bird species.
Table S4.2	Current and future probabilities of occurrence derived from SDMs for all 240 frugivorous bird species.
Table S4.3	Model evaluation metrics for each bird species and SDM algorithm.
Figure S4.1	Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range contraction scenario*, RCP 6.0.
Figure S4.2	Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range shift scenario*, RCP 6.0.
Figure S4.3	Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range expansion scenario*, RCP 8.5.
Figure S4.4	Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range contraction scenario*, RCP 8.5.
Figure S4.5	Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range shift scenario*, RCP 8.5.



Chapter 5

General discussion

GENERAL DISCUSSION

In this thesis, I explore how functional traits influence species interactions and how functional trait diversity could potentially be affected by climate change. This thesis contributes to our understanding of the relationship between functional roles and traits of species in seed dispersal networks. It also provides insights into the possible repercussions of climate change on the functional diversity of frugivorous birds along elevational gradients. Throughout the three presented studies, I considered the functional diversity of seed dispersal communities from three different perspectives. I focused on the seasonal variation in functional diversity (chapter 2), spatial variation in functional diversity (chapter 3), and finally used future projections to provide insights into the potential future functional composition of frugivore communities (chapter 4) in the tropical Andes.

First, I explored the response of frugivorous birds to seasonal variation in fruit availability (chapter 2). I focused on the functional role of the birds in the networks, and specifically studied the flexibility with which birds are able to switch between fruit resources. As expected, I found that the degree of functional specialization of bird species was rather constant throughout the year. The degree of functional specialization was positively related to functional flexibility. This indicates that the species with the highest degree of functional specialization were also the species with the highest flexibility to change to alternative types of fruit resources.

To test how general trait matching is in interactions between fleshy-fruited plant and frugivorous birds, I explored the spatial variation of trait matching and functional specialization (chapter 3). I showed that traits related to size matching and traits related to animal foraging were equally important in shaping interactions between plants and birds in the Andes. This result is important since it provides the first step on the way to the deduction of general interaction rules. It provides the basis for predicting unknown interactions from species' functional traits in novel ecological communities (Kissling and Schleuning 2015), for instance as a result of species' migrations and local extinctions in response to climate change.

Finally, the future projections in chapter 4 contributed insights into potential changes in functional diversity of frugivore communities. The results indicate that communities at different elevations along a tropical mountain might be affected in different ways. The projected functional attrition in the lowland bird communities would impose severe constraints for lowland plant communities, due to the loss of animal seed dispersers. At mid-elevations, bird communities were projected to reshuffle. This would lead to functional turnover in communities at different elevations and for the lower mid-elevations even an increase in functional diversity, due to immigrating lowland species. These changes would require interactions between birds and plants to rewire in projected future communities.

SPECIES INTERACTIONS

Functional traits are extremely important for species interactions. This has been found in seminal work by Wheelwright (1985) and Jordano (1987) and has been supported and reinforced by the scientific world ever since. Over the last decades, research has increasingly focused on identifying the functional traits that mediate the matching of interaction partners (*e.g.*, Woodward and Warren 2007, Stang *et al.* 2006, 2009, Eklöf *et al.* 2013, Dehling *et al.* 2014b, Garibaldi *et al.* 2015, Maglianesi *et al.* 2015, Bartomeus *et al.* 2016). In this thesis, I showed that traits from interacting partners were generally correlated across interaction networks on a large spatial scale (chapter 3). The degree of trait matching was consistent across the sub-tropics and the tropics and from 1000 m to 3000 m elevations. While this study only compared seed dispersal systems between birds and plants, the generality found here suggests that this might extend to different types of mutualisms. Indeed, the generality of trait matching has also been shown in plant-pollination networks (*e.g.*, Garibaldi *et al.* 2015) where interactions are highly influenced by the matching of, *e.g.*, proboscis/bill length and corolla length/nectar depth (Stang *et al.* 2009, Maglianesi *et al.* 2015). An interesting next step would be to combine these various interaction types, such as seed dispersal and pollination, into one meta-analysis that could compare the strength of trait matching among different interaction types.

The strength of using a functional approach in the analysis of interaction networks calls for different, complementary concepts for the description of functional roles in these communities. While there is previous work on functional roles in interaction networks (Waser and Ollerton 2006, Olesen *et al.* 2011a, Schleuning *et al.* 2015, Dehling *et al.* 2016), this thesis offers new insights into the description of functional roles based on functional traits and the community context (chapter 2). One interesting aspect of this functional description is that it could be used to compare the functional roles among different taxa. The methodology proposed could, for instance, be applied to an interaction network of fleshy-fruited plants and all their dispersal agents, including both birds *and* mammals. This would allow a direct comparison of functional roles of different taxa and the degree to which, *e.g.*, mammals would be able to compensate for the loss of bird species (Mello *et al.* 2011, Dehling *et al.* 2016).

The suitability of functional trait data for the determination of the functional roles of species was further confirmed by the finding that functional roles, based on the matching of traits, were seasonally stable (chapter 2). The seasonal stability indicates that, even though functional specialization was measured from a community perspective, it still seems to be conserved across different contexts. In addition, the relationship between functional traits and the degree of functional specialization might make it possible to identify those bird and plant species that fulfill particular functional roles by their traits (chapter 3). Mello *et al.* (2015) already described that dietary specialization is the most important trait identifying frugivorous keystone species. My results go one step further and provide a framework to identify keystone species by their traits. This identification can be highly useful, as the loss of keystone species would have severe effects on biotic interactions, community dynamics and forest structure (Galetti *et al.* 2013, Dirzo *et al.* 2014, Vidal *et al.* 2014).

The functional roles, as determined by specific functional traits, are also phylogenetically conserved (chapter 2). This finding adds to previous work that indicated that the phylogenetic position of a species influences the species degree, *i.e.*, the number of interaction partners of a species (Rezende *et al.* 2007, Kissling and Schleuning 2015), and the species position within network modules (Schleuning *et al.* 2014). This phylogenetic clustering of functional roles might render specific functional roles especially vulnerable, since extinction events could trigger coextinction cascades of related species (Rezende *et al.* 2007). This non-random loss of species could, therefore, lead to the loss of an entire functional role from the community, which consequently will affect ecosystem functioning (Şekercioğlu 2011, Galetti *et al.* 2013).

In mutualistic interactions, species depend on the availability of suitable interaction partners. Therefore, the loss of species in one community will affect the partner community as well. For example, my results (chapter 4) revealed strong support for the hypothesis that the frugivore community in the lowlands will be severely affected by climate change. The extinction of bird species in these environments might lead to a cascade of extinctions in the plant community through secondary extinctions (Colwell *et al.* 2012, Brodie *et al.* 2014). However, not all species will be equally vulnerable to secondary extinctions (Schleuning *et al.* 2016). It is likely that species which interact with many different partners are less vulnerable to secondary extinction. Yet, secondary extinctions might be better measured by the cumulative risk of all the partners (Rezende *et al.* 2007, Brodie *et al.* 2014), especially when all partners are phylogenetically and/or functionally related. I have identified a mechanism that might act as a buffer to secondary losses of species, *i.e.*, functional flexibility (chapter 2). Having the capacity to interact with a range of functionally distinct species might protect a species from the loss of all their interaction partners. Since my work indicated that the most functionally flexible species were also the species with the highest degree of functional specialization (*e.g.*, birds with pointed wings that provide long-distance dispersal to plant communities, chapter 3), this might be an especially important finding that could contribute to ecosystem stability in the future.

Apart from species extinctions, global change might lead to the reshuffling of communities (chapter 4). Species migrations can lead to simultaneous emigration and immigration of species. The resulting increase and/or turnover in functional composition in these communities implies challenges for these communities. The perseverance of species in a new community depends primarily on the presence of suitable interaction partners (Poisot *et al.* 2015), and secondarily on the potential of species to form new interactions and rewire the network. If we are able to infer the likelihood that an interaction between two species will take place, based on their morphology and interaction preferences, then we would be able to predict whether interactions between new partners could rewire under future conditions (Morales-Castilla *et al.* 2015, Bartomeus *et al.* 2016, Dehling *et al.* 2016). Evidence that species are capable of rewiring and interacting with species in a new community comes from research on invasive species: newly arriving species are usually rapidly included in mutualistic interaction networks (Morales and Aizen 2006, Bartomeus *et al.* 2008, Burkle and Alarcón 2011, Olesen *et al.* 2010). A high potential for rewiring in novel communities could thus be another stabilizing mechanism of interaction networks under future conditions.

FUNCTIONAL DIVERSITY

Exploring community level functionality is most aptly done with functional diversity metrics. More simple metrics, like number of species, fail to account for the functional differences between species (Winfree and Kremen 2009, Flynn *et al.* 2009). Community level functional diversity, on the other hand, can be directly linked to ecosystem functioning (*e.g.*, Díaz and Cabido 2001, Lavorel and Garnier 2002, Hooper *et al.* 2005, Flynn *et al.* 2009, Reiss *et al.* 2009, Gagic *et al.* 2015, Lavabre *et al.* 2016). To rigorously apply functional diversity depends on the knowledge of the functionally relevant traits (Violle *et al.* 2007). In my studies, I was able to use in-depth knowledge acquired by Dehling *et al.* (2014b, 2016) on the functional traits that are relevant for shaping plant-frugivore interactions. Based on these findings, I could show the strength of using functional approaches in the analysis of seed dispersal networks (chapter 2-4), *e.g.*, by demonstrating the functional flexibility of functional specialists, and the generality of trait matching across the Andes.

Functional diversity metrics provide a comprehensive evaluation of the ecosystem function of seed dispersal (Tilman 2001, Gagic *et al.* 2015, Schleuning *et al.* 2015). However, the various species contribute to different degrees to the overall functioning of the community, through differences in their direct (*e.g.*, higher degree of functional specialization, chapter 2-4, Dehling *et al.* 2016, Mello *et al.* 2015, Sebastián-González 2017) or indirect (*e.g.*, via competition and facilitation, Martínez *et al.* 2014, Albrecht *et al.* 2015, Donoso *et al.* 2017) effects on the ecosystem. Functional diversity metrics could be further enhanced by adding additional information to the assessment of functional diversity, which can account for these differences between species (chapter 4, Barbet-Massin and Jetzt 2015). Such additional information could be data on species abundance or on the probability that a species occurs in a community. The ecological neighborhood (*i.e.*, the indirect effect of other local species sharing traits and interaction potential with the focal species, Donoso *et al.* 2017) has been shown to influence pairwise interaction frequency in plant-frugivore networks (Martínez *et al.* 2014, Albrecht *et al.* 2015, González-Castro *et al.* 2015, Donoso *et al.* 2017). Hence, weighing species differently in the calculation of functional diversity can make the description of the function of interest better *and* improve the capability of these metrics to indicate functional changes.

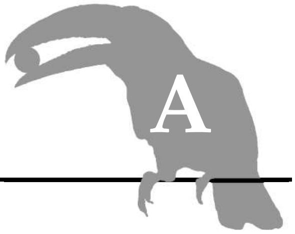
While functional traits can help to quantify the functional role of species, functional diversity metrics can quantify the effect of the loss or gain of specific species for the community (*e.g.*, Larsen *et al.* 2005). Dehling *et al.* (2016) showed that the locations of avian frugivores in functional trait space match their respective locations in resource trait space. This implies that the loss of functional diversity of the bird community corresponds directly to a loss of seed dispersal functions in the plant community. Typically, functionally specialized species are located at the edges of the community trait space (chapter 2), a position that greatly affects functional diversity. These species are often unique in their contribution to ecosystem functioning, *e.g.*, pointed winged birds that contribute to long-distance dispersal (Böhning-Gaese *et al.* 2006). Similarly, this might apply to all types of functions that are mediated by interactions.

As discussed before, functional flexibility of specialized species could provide a buffer from extinction. Nevertheless, the functionally specialized roles that these species fulfill in the community might still be the most threatened functional roles (Clavel *et al.* 2011). Species with low degrees of functional specialization and less specialized functional roles, have a higher degree of functional redundancy in the community, making these roles less prone to be lost. Hence, the loss of a functionally redundant species will result in little loss of community functioning, because many other species fulfill similar roles (Flynn *et al.* 2009). On the contrary, functionally specialized species lack functional redundancy, meaning that no or few other species could substitute for them in cases where they became locally extinct (Dehling *et al.* 2016, Mello *et al.* 2015, Sebastián-González 2017). These functional specialists, *e.g.*, large-bodied frugivores, are also more vulnerable to drivers of change (Gaston and Blackburn 1995), such as, *e.g.*, land-use change (Flynn *et al.* 2009), habitat disturbance (Bregman *et al.* 2016) and hunting (Peres and Palacios 2007). The vulnerability of functional specialists to change has been found in other interaction types as well (*e.g.*, pollination networks, Larsen *et al.* 2005). The loss of these species would have a large effect on community functionality and could lead to functional homogenization in ecological communities (Clavel *et al.* 2011).

CONCLUSIONS

The results presented in this thesis contribute to the overall understanding of the functional roles that different species contribute to the functioning of ecosystems. I discussed how functional traits influence species interactions and how functional diversity might change under climate change. Understanding these processes can help to better understand the spatial and temporal dynamics of mutualistic seed dispersal interactions in the tropics. While I focused on this interaction system, the concepts and theories provided in this thesis are applicable beyond the scope of seed dispersal interaction networks. My thesis therefore directly contributes to the theoretical knowledge of the functionality of interaction networks, and specifically to the understanding of the functional roles that species contribute to the ecological communities.

It is undeniable that climate change will lead to changes in ecological communities. An important challenge will be to understand how these changes will affect the future of biodiversity and ecosystem functioning (Loreau *et al.* 2001, Tylianakis and Morris 2017). Species are already changing their ranges and distributions (Colwell *et al.* 2008), which suggests that future communities will experience a turnover in species composition. These new communities will need to reassemble in the future. This leads to the question of whether communities will break down, or restructure and persevere. Based on the results that I have presented in this thesis, I expect that communities of interacting species will be able to reassemble in the future. While the severity of anthropogenic climate change is unprecedented, climate fluctuations have always been a natural phenomenon (Crowley 2000). It is therefore likely that ecological communities have experienced changes in species composition in the past. Stabilizing mechanisms, such as functional flexibility, will aid ecological communities to adjust to changes in species composition. So, even though the fates of individual species might be dire due to dispersal limitations or the inability to find new interaction partners, the overall community might be able to restructure, rewire, and persist. Functional roles might be fulfilled by different species in these future communities, but the ecological function is likely to be performed. However, the capacity of ecological communities to adapt to future changes is limited if the combined impacts of different drivers of global change lead to a functional homogenization of communities. Improvement of the knowledge on how communities will adjust, and to what extend this will be possible, is crucial to understand how ecological communities will function in the future.



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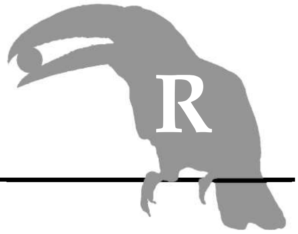

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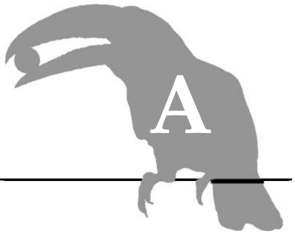

Appendices

Curriculum vitae

Publications & Conferences

Authors’ contributions

Eigenständigkeitserklärung

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2013 - Present **Doctoral student**
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Received at the FSD conference in South Africa (2015)

PUBLICATIONS OF THE DISSERTATION

Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Wiegand, T., Dehling, D.M. & Schleuning, M. (2017) Functionally specialised birds respond flexibly to seasonal changes in fruit availability. *Journal of Animal Ecology*, **86**, 800–811.

Bender, I.M.A., Kissling, W.D.K., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitian, M., Saavedra, F., Santillan, V., Töpfer, T., Wiegand, T., Dehling, D.M.D. & Schleuning, M. (Manuscript) Morphological trait matching shapes plant-frugivore networks across the Andes. (*Ecography*, *under review since 28-08-2017*)

Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Nowak, L., Töpfer, T., Wiegand, T., Dehling, D.M. & Schleuning, M. (Manuscript) Effects of climate change on functional diversity of birds on a tropical mountain. (*submitted to Nature Communications on 04-12-2017*)

ADDITIONAL PUBLICATIONS

Sarneel, J.M., Janssen, R.H., Rip, W.K., **Bender, I.M.A.** & Bakker, E.S. (2014) Windows of opportunity for germination of riparian species after restoring water level fluctuations: A field experiment with controlled seed banks. *Journal of Applied Ecology*, **51**, 1010–1014.

CONTRIBUTION TO CONFERENCES

Bender, I.M.A., Kissling, W.D.K., Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitian, M., Saavedra, F., Santillan, V., Töpfer, T., Wiegand, T., Dehling, D.M.D. & Schleuning, M. (2017) Identifying plant and animal traits shaping plant-frugivore networks across the Andes. *Netherlands Annual Ecology Meeting (NAEM)*, Lunteren, the Netherlands. Oral presentation.

Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Wiegand, T., Dehling, D.M. & Schleuning, M. (2016) Feeding originality and flexibility of birds in plant-frugivore interaction networks. *Meeting of the Society of Tropical Ecology (GTÖ)*, Göttingen, Germany. Oral presentation.

Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Wiegand, T., Dehling, D.M. & Schleuning, M. (2015) Feeding originality and flexibility of birds in plant-frugivore interaction networks. *Frugivores and Seed Dispersal (FSD) conference 2015*, Drakensberg, South Africa. Oral presentation, receiver of the "Best oral presentation" award.

Bender, I.M.A., Kissling, W.D., Hensen, I., Kühn, I., Wiegand, T., Dehling, D.M. & Schleuning, M. (2014) Effects of climate change on mutualistic networks in a tropical diversity hotspot. *Joint annual meeting of the British Ecological Society (BES) and French Ecological Society (SFÉ)*, Lille, France. Poster presentation.

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CHAPTER 2

Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Wiegand, T., Dehling, D.M. & Schleuning, M. (2017) Feeding originality and flexibility of birds in plant-frugivore interaction networks. *Journal of Animal Ecology*, 86, 800–811.

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Dehling, D.M. (50%)

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Data analysis

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Preparation of manuscript

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Blendinger, P.G., Böhning-Gaese, K., Hensen, I., Kühn, I., Muñoz, M.C., Neuschulz, E.L., Nowak, L., Quitian, M., Saavedra, F., Santillan, V., Töpfer, T., Wiegand, T. (5%)

CHAPTER 4

Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Nowak, L., Töpfer, T., Wiegand, T., Dehling, D.M. & Schleuning, M. (Manuscript) Effects of climate change on functional diversity of birds on a tropical mountain. (*submitted 04-12-2017*)

Development & planning

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Data collection & compilation

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Töpfer, T. (10%)

Data analysis

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Preparation of manuscript

Bender, I.M.A. (75%)
Schleuning, M., Kissling, W.D. (20%)
Böhning-Gaese, K., Dehling, D.M., Hensen, I., Kühn, I., Nowak, L., Töpfer, T., Wiegand, T. (5%)

Frankfurt am Main, den 05-12-2017

Irene M.A. Bender

EIGENSTÄNDIGKEITSERKLÄRUNG

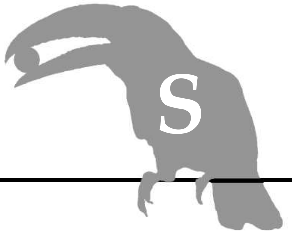
Hiermit erkläre ich, dass die Arbeit mit dem Titel „Functional diversity and mutualistic interactions of frugivorous birds in the Tropical Andes“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Frankfurt am Main, den 05-12-2017

Irene M.A. Bender

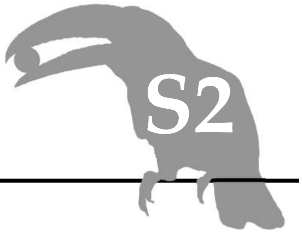


Supplement materials

Supplement materials Chapter 2

Supplement materials Chapter 3

Supplement materials Chapter 4



S2

Supplement materials

Chapter 2

FUNCTIONALLY SPECIALIZED BIRDS RESPOND FLEXIBLY TO SEASONAL CHANGES IN FRUIT AVAILABILITY

Irene M.A. Bender, W. Daniel Kissling, Katrin Böhning-Gaese, Isabell Hensen, Ingolf Kühn, Thorsten Wiegand, D. Matthias Dehling and Matthias Schleuning (2017) *Journal of Animal Ecology*, **86**, 800–811.

Figure S2.1	Seasonal interaction networks between frugivorous birds and fleshy fruited plants were collected at San Pedro (1500 m.a.s.l.) and at Wayqecha (3000 m.a.s.l.) in Manu, Peru.
Figure S2.2	Plant trait space across 99 plant species in the Peruvian Andes.

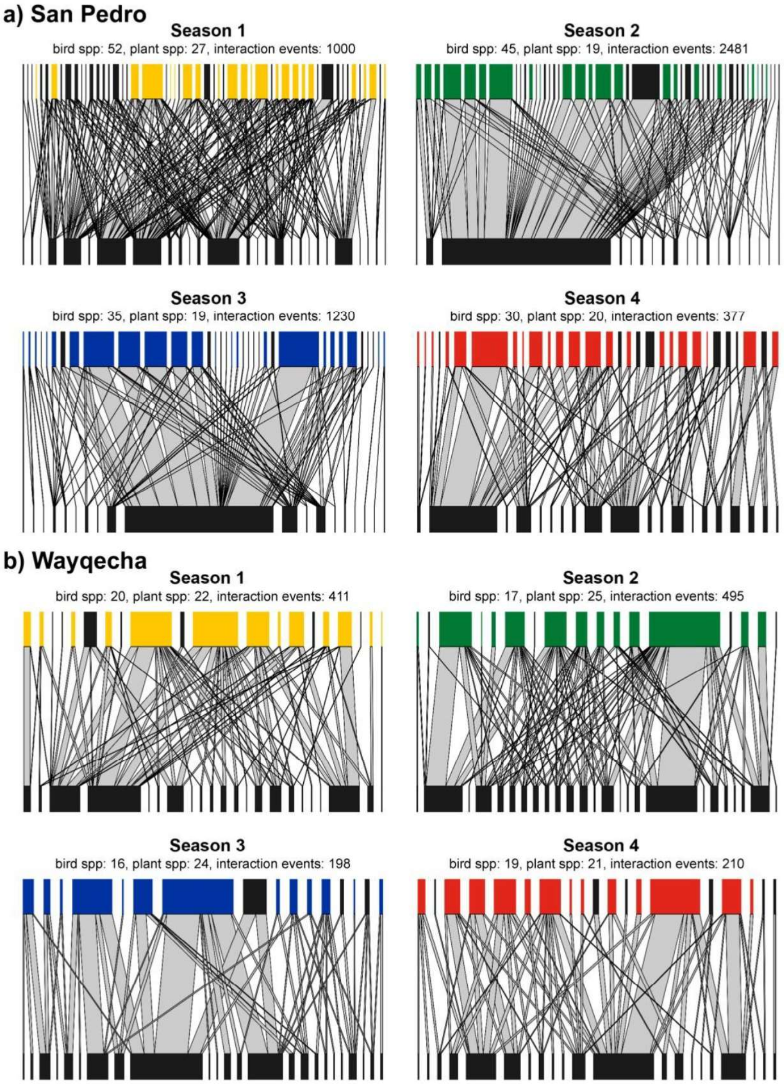


Figure S2.1. Seasonal interaction networks between frugivorous birds and fleshy fruited plants were collected at San Pedro (1500 m.a.s.l.) and at Wayqecha (3000 m.a.s.l.) in Manu, Peru. Data were collected from December 2009 to September 2010, approximately every three months. Season one (yellow) and two (green) cover the beginning and peak of the rainy season, season three (blue) and four (red) the beginning and peak of the dry season. Bird and plant species are represented by boxes at the top and bottom, respectively. Interactions between species are indicated by lines between boxes and box size indicates the respective interaction strength. Coloured boxes indicate frugivorous species represented in all four seasons of one or both of the networks and were considered for the analyses of this manuscript. The proportion of interactions contributed by these species to the total network, compared to the other species was high in both San Pedro (season 1; 0.69, season 2; 0.74, season 3; 0.93, season 4; 0.61) and in Wayqecha (season 1; 0.96, season 2; 0.98, season 3; 0.85, season 4; 0.92). Number of bird species, plant species and interactions events is given for each seasonal network.

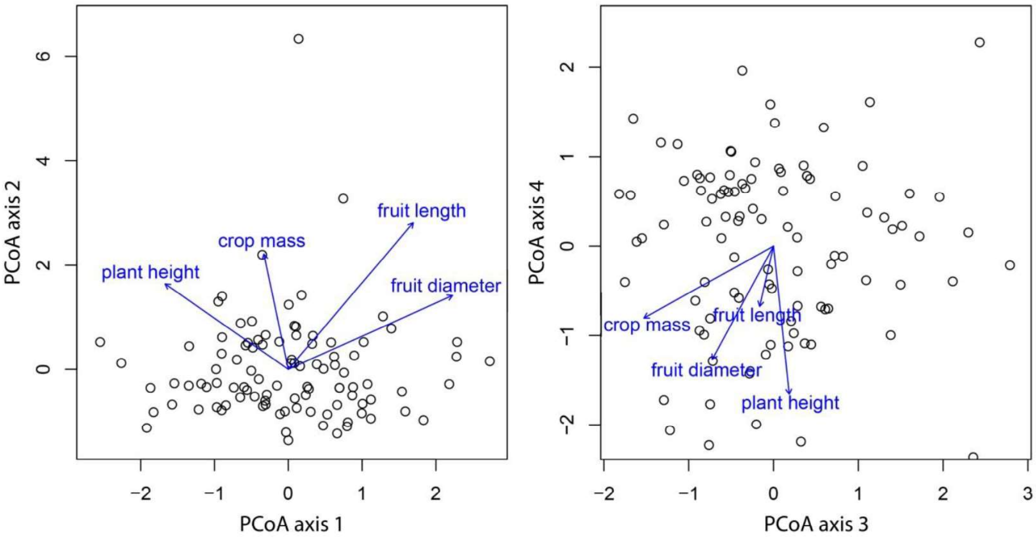
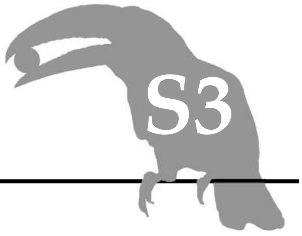


Figure S2.2. Plant trait space across 99 plant species in the Peruvian Andes. Shown are all four axes of the plant trait space as derived from a principal coordinate analysis (PCoA) on Mahalanobis distances between species. Dots represent the 99 plant species observed across the four seasons at San Pedro (1500 m.a.s.l.) and at Wayqecha (3000 m.a.s.l.) in Manu, Peru. Blue arrows indicate the relationship between the PCoA axes and the four original morphological plant traits (*i.e.*, fruit length, fruit diameter, plant height and crop mass); the length of the arrows is proportional to the strength of the relationship with the respective axes.



Supplement materials

Chapter 3

Morphological trait matching shapes plant-frugivore networks across the Andes

Irene M.A. Bender, W. Daniel Kissling, Pedro G. Blendinger, Katrin Böhning-Gaese, Isabell Hensen, Ingolf Kühn, Marcia C. Muñoz, Eike Lena Neuschulz, Larissa Nowak, Marta Quitián, Francisco Saavedra, Vinicio Santillán, Till Töpfer, Thorsten Wiegand, D. Matthias Dehling and Matthias Schleuning. *Ecography* (*under review since 28-08-2017*)

Supplement 3.1	Sampling of the interaction networks.
Table S3.1	Comparison between the meta-analyses weighted by sampling effort and sampling completeness.
Figure S3.1	Accumulation curves and asymptotic bird richness for the eight interaction networks across the Andes.
Figure S3.2	Accumulation curves and asymptotic link richness (*i.e.*, the number of interacting species pairs) for the eight interaction networks across the Andes.
Figure S3.3	Fourth-corner correlations between functional traits of frugivorous bird species and fleshy-fruited plant species across the Andes.

SUPPLEMENT 3.1: SAMPLING OF THE INTERACTION NETWORKS

Colombia

We collected interaction networks of frugivorous birds and fleshy-fruited plants at two sites in the Andes of Central Colombia (Munoz *et al.* 2017). Network Colombia 1 was collected at Santuario de Flora y Fauna Otún Quimbaya in a high montane forest at 1800 m a.s.l. (hereafter "m"). Network Colombia 2 was collected at Parque Regional Ucumari in upper montane forest at 2700 m.

At each location, we collected data during four time periods. Sampling was done approximately every three months between February 2012 and November 2012, resulting in four temporal replicates of each network. Two replicates cover the rainy season (May and November) and two replicates the dry season (February and August). We recorded fruit removal by frugivorous birds on all fleshy-fruited plant species located in 100 m × 20 m plots (five plots in Santuario, five plots in Ucumari). During each time period, every plot was observed on five consecutive days between dawn and noon for a total of 30 hours. The total observation time was 600 h in Colombia 1 and 600 h in Colombia 2.

Ecuador

We sampled interaction networks of frugivorous birds and fleshy-fruited plants in and around Podocarpus National Park in the south Ecuadorian Andes. Network Ecuador 1 was sampled in an evergreen premontane forest at 1000 m. Network Ecuador 2 was sampled in a lower montane forest at 2000 m.

We sampled plant-frugivore interactions four times in 2014 and 2015, twice in the most humid season (May to July) and twice in the least humid season (October to December), resulting in four temporal replicates of each network. We recorded seed removal by frugivorous birds on all fleshy-fruited plant species located in 100 m × 30 m plots (three plots at every elevation). During each time period, every plot was observed on five consecutive days between dawn and noon for a total of 25 hours. The total observation time was 300 h for Ecuador 1 and 300 h for Ecuador 2.

Peru

We collected interaction networks of frugivorous birds and fleshy-fruited plants at two sites in the Andes of south-east Peru (Dehling *et al.* 2014). Network Peru 1 was collected in lower montane forest at 1500 m. Network Peru 2 was collected in upper montane forest at 3000 m. At each location, we collected data during four time periods. Sampling was done approximately every three months between December 2009 and September 2010, resulting in four temporal replicates of each network. The first two replicates cover the beginning and peak of the rainy season, the third and fourth replicate the beginning and peak of the dry season, respectively. We recorded seed removal by frugivorous birds on all fleshy-fruited plant species located in 100 m × 30 m plots (eight plots in San Pedro, six plots in Wayqecha). During each time period, every plot was observed on five consecutive days between dawn and noon for a total of 30 hours. The total observation time was 960 h in Peru 1 and 720 h in Peru 2 (Dehling *et al.* 2014).

Bolivia

We collected interaction networks of frugivorous birds and fleshy-fruited plants at two sites in the Andes of South West Bolivia (Saavedra *et al.* 2014). Network Bolivia was collected in the vicinity of Chulumani town in upper montane forest at 2500 m. We collected data during four observation sessions, conducted during two dry seasons and two wet seasons between June 2010 and February 2012. We recorded seed removal by frugivorous birds on all fleshy-fruited plant species located in 100 m × 20 m plots (eight plots overall). During each observation session, every plot was simultaneously observed by two observers on two consecutive days from 06:00 a.m. to 12:00 p.m. for a total of 24 hours. The total observation time was 768 h.

Argentina

We collected interaction networks of fruit-eating birds and fleshy-fruited plants at one site in the Andes of north-west Argentina (Blendinger *et al.* 2012, 2015). Network Argentina was collected at Parque Sierra de San Javier, Tucumán, in montane forest at 1000 m. We collected data during twelve time periods. Sampling was done bi-monthly between September 2008 and August 2010, resulting in twelve temporal replicates of the network (Blendinger *et al.* 2012, 2015), six during the first sampling year (September to July) and six during the second sampling year (October to August). We recorded fruit removal by fruit-eating birds on all fleshy-fruited plant species located in a 300 m × 200 m plot. At each time period, during three sampling days, five observers traversed a block of 10 x 2 contiguous 20 x 20-m cells and recorded all fruit-consumption events for 20 min per cell. The total observation time was 600 h.

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Dehling, D.M., Töpfer, T., Schaefer, H.M., Jordano, P., Böhning-Gaese, K. & Schleuning, M. (2014) Functional relationships beyond species richness patterns: trait matching in plant-bird mutualisms across scales. *Global Ecology and Biogeography*, **23,** 1085–1093.

Muñoz, M.C., Schaefer, H.M., Böhning-Gaese, K., Neuschulz, E.L. & Schleuning, M. (2017) Phylogenetic and functional diversity of fleshy-fruited plants are positively associated with seedling diversity in a tropical montane forest. *Frontiers in Ecology and Evolution*, **5**, 93.

Saavedra, F., Hensen, I., Beck, S.G., Böhning-Gaese, K., Lippok, D., Töpfer, T. & Schleuning, M. (2014) Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia*, **176**, 837–848.

Table S3.1. Meta-analyses of fourth-corner correlations between traits of plants and frugivores across eight Andean networks. Meta-analysis (1) was weighted by sampling effort (*i.e.*, the square-root of the total number of observed interactions per network), while meta-analysis (2) was weighted by sampling completeness (*i.e.*, the observed link richness divided by the asymptotic richness based on the Chao estimator). Shown are model estimate (*Z mean*) and their respective standard errors (*SE*) and *P*-values.

	Meta-analysis (1) weighted by sampling effort			**Meta-analysis (2) weighted by sampling completeness**		
Traits	*Z mean*	*SE of Z*	*P*	*Z mean*	*SE of Z*	*P*
Fruit diameter ~ Bill width	0.32	0.07	< 0.001	0.29	0.07	< 0.001
Fruit length ~ Bill length	0.26	0.07	< 0.001	0.25	0.07	< 0.001
Plant height ~ Wing shape	0.33	0.06	< 0.001	0.29	0.04	< 0.001
Crop mass ~ Body mass	0.21	0.10	0.02	0.18	0.10	0.03

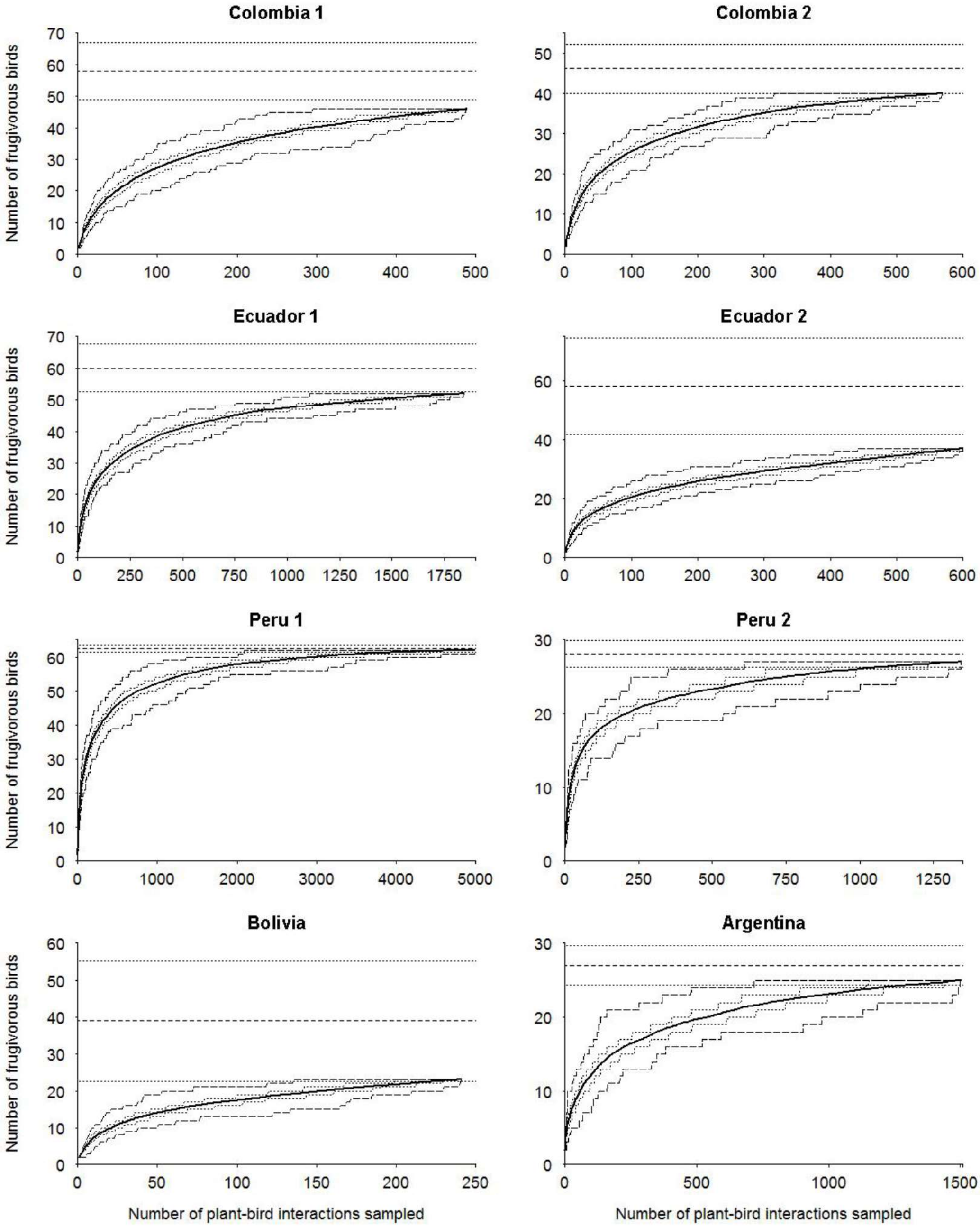


Figure S3.1. Accumulation curves of estimated bird richness for the eight interaction networks across the Andes. Dotted lines around the accumulation curves show the first and third quartiles and the standard errors, respectively; dashed lines show the asymptotic total richness with standard errors based on the Chao richness estimator (Oksanen *et al*. 2015).

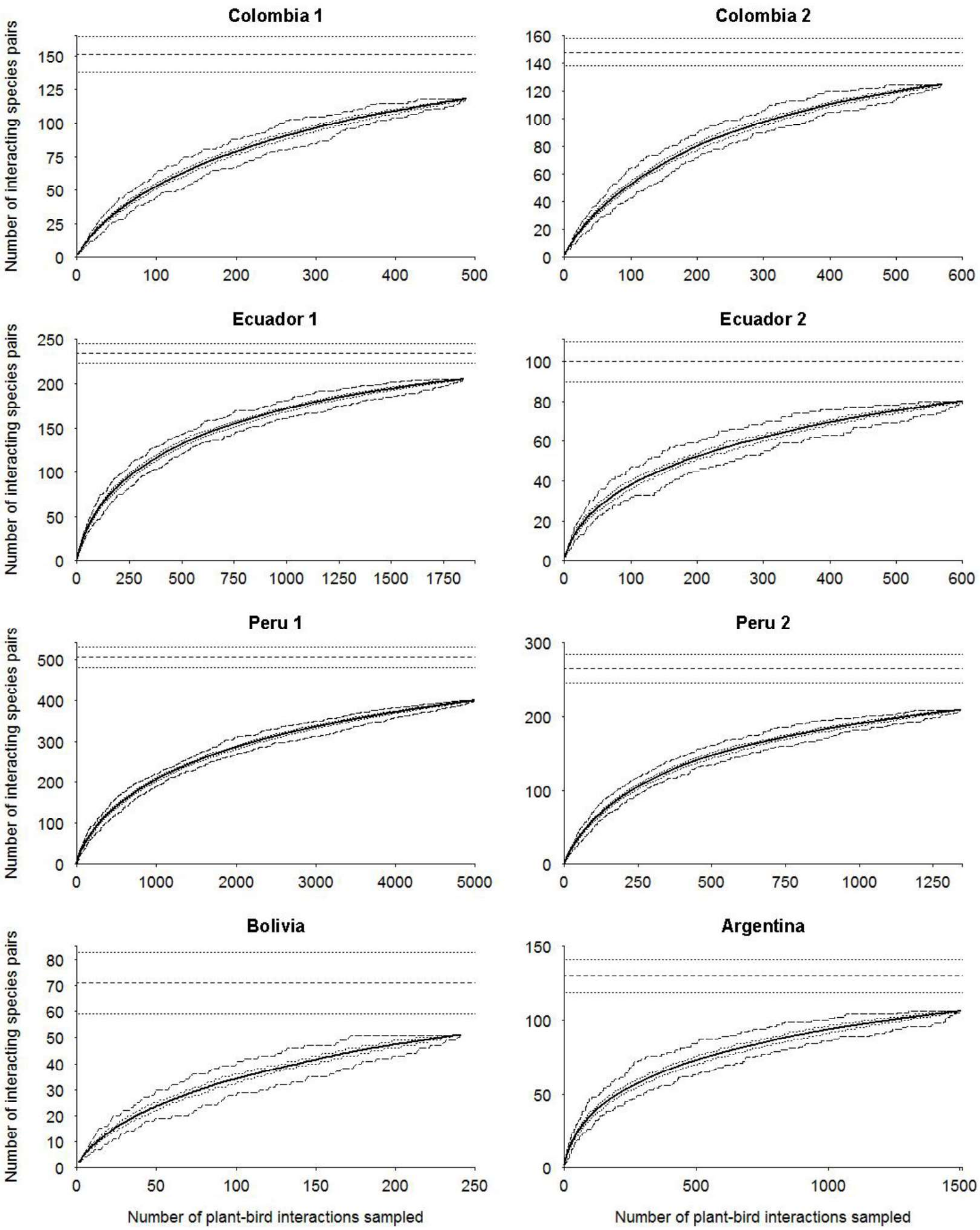


Figure S3.2. Accumulation curves of estimated link richness (*i.e.*, the number of interacting species pairs) for the eight interaction networks across the Andes. Dotted lines around the accumulation curves show the first and third quartiles and the standard errors, respectively; dashed lines show the asymptotic link richness with standard errors based on the Chao richness estimator (Oksanen *et al.* 2015).

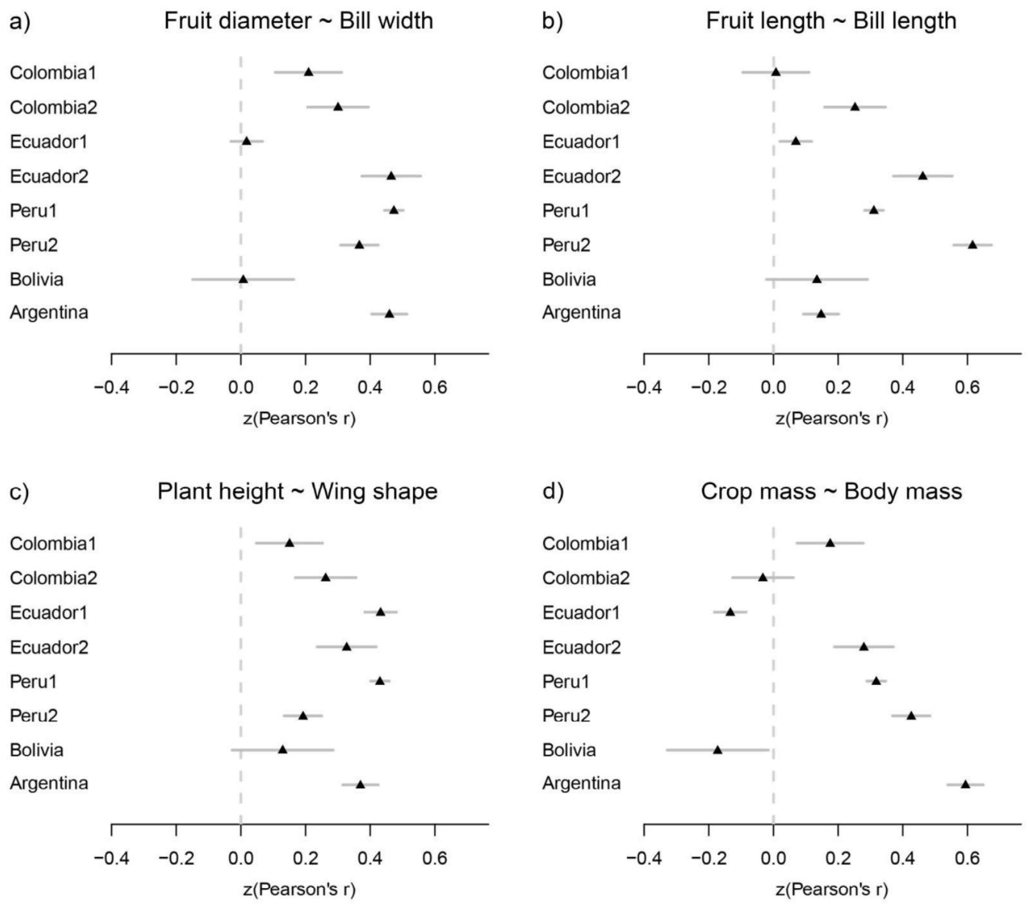
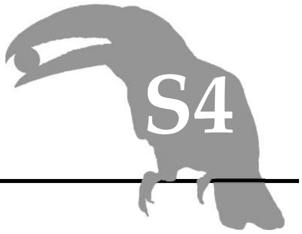


Figure S3.3. Fourth-corner correlations between functional traits of frugivorous bird species and fleshy-fruited plant species across the Andes. Correlations of four trait pairs were tested in eight interaction networks across the Andes. The four analysed trait-pairs were; (a) fruit diameter and bill width, (b) fruit length and bill length, (c) plant height and wing shape, (d) crop mass and body mass. Triangles indicate the z-transformed Pearson's correlation coefficient *r* from the fourth-corner analysis; grey lines indicate the variance of the correlation coefficient derived from the square-root number of observed interaction events in each network.



S4

Supplement materials

Chapter 4

EFFECTS OF CLIMATE CHANGE ON FUNCTIONAL DIVERSITY OF BIRDS ON A TROPICAL MOUNTAIN

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Table S4.1 Current and future elevational ranges of all 240 frugivorous bird species of the Manú Biosphere Reserve, Peru, based on the MIROC5 climate model.

Table S4.2 Current and future probabilities of occurrence derived from SDMs of all 240 frugivorous bird species of the Manú Biosphere Reserve, Peru, based on the MIROC5 climate model.

Table S4.3 Model evaluation metrics for each bird species and SDM algorithm.

Figure S4.1 Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range contraction scenario*, RCP 6.0.

Figure S4.2 Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range shift scenario*, RCP 6.0.

Figure S4.3 Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range expansion scenario*, RCP 8.5.

Figure S4.4 Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range contraction scenario*, RCP 8.5.

Figure S4.5 Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range shift scenario*, RCP 8.5.

Table S4.1. Current and future elevational ranges of all 240 frugivorous bird species of the Manú Biosphere Reserve, Peru, based on the MIROC5 climate model. Current elevational ranges and bird taxonomy are derived from Dehling et al. (2014a). Future elevational ranges were projected based on vertical distance movements of each bird species based on future temperature scenarios and tropospheric lapse-rates. Three potential migration scenarios were considered: range contraction (where the lower range limit moves upwards), range expansion (where the upper range limit moves upwards), and range shift where both the lower and upper range limit move upwards.

		Current		**Range expansion**			**Range contraction**			**Range shift**			
					RCP 6.0	**RCP 8.5**	**RCP 6.0**	**RCP 8.5**		**RCP 60**		**RCP 8.5**	
Family	**Bird species**	**min**	**max**	**min**	**max**	**max**	**min**	**min**	**max**	**min**	**max**	**min**	**max**
Cardinalidae	*Cyanocompsa cyanoides*	250	1400	250	1786	1953	636	803	1400	636	1786	803	1953
Cardinalidae	*Pheucticus aureoventris*	600	3250	600	3622	3774	972	1124	3250	972	3622	1124	3774
Cardinalidae	*Pheucticus chrysogaster*	650	3500	650	3869	4023	1019	1173	3500	1019	3869	1173	4023
Cardinalidae	*Saltator aurantiirostris*	2600	3500	2600	3864	4026	2964	3126	3500	2964	3864	3126	4026
Cardinalidae	*Saltator coerulescens*	250	900	250	1294	1463	644	813	900	644	1294	813	1463
Cardinalidae	*Saltator grossus*	250	1006	250	1392	1559	636	803	1006	636	1392	803	1559
Cardinalidae	*Saltator maximus*	250	2507	250	2886	3042	629	785	2507	629	2886	785	3042
Columbidae	*Geotrygon montana*	250	1489	250	1875	2042	636	803	1489	636	1875	803	2042
Columbidae	*Patagioenas cayennensis*	250	900	250	1294	1463	644	813	900	644	1294	813	1463
Columbidae	*Patagioenas fasciata*	1200	3530	1200	3899	4051	1569	1721	3530	1569	3899	1721	4051
Columbidae	*Patagioenas plumbea*	250	1991	250	2374	2535	633	794	1991	633	2374	794	2535
Columbidae	*Patagioenas subvinacea*	250	1550	250	1933	2094	633	794	1550	633	1933	794	2094
Corvidae	*Cyanocorax cyanomelas*	250	1100	250	1486	1653	636	803	1100	636	1486	803	1653
Corvidae	*Cyanocorax violaceus*	250	1400	250	1786	1953	636	803	1400	636	1786	803	1953
Corvidae	*Cyanocorax yncas*	1150	2200	1150	2572	2718	1522	1668	2200	1522	2572	1668	2718
Cotingidae	*Ampelioides tschudii*	700	1400	700	1771	1932	1071	1232	1400	1071	1771	1232	1932
Cotingidae	*Ampelion rubrocristatus*	2500	3450	2500	3822	3976	2872	3026	3450	2872	3822	3026	3976
Cotingidae	*Ampelion rufaxilla*	1600	2850	1600	3222	3368	1972	2118	2850	1972	3222	2118	3368
Cotingidae	*Cephalopterus ornatus*	250	1650	250	2033	2194	633	794	1650	633	2033	794	2194
Cotingidae	*Conioptilon mcilhennyi*	250	450	250	852	1029	652	829	450	652	852	829	1029
Cotingidae	*Cotinga cayana*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Cotingidae	*Cotinga maynana*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Cotingidae	*Gymnoderus foetidus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Cotingidae	*Iodopleura isabellae*	250	850	250	1244	1413	644	813	850	644	1244	813	1413
Cotingidae	*Laniocera hypopyrra*	250	750	250	1144	1313	644	813	750	644	1144	813	1313
Cotingidae	*Lipaugus vociferans*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Cotingidae	*Oxyruncus cristatus*	850	1300	850	1671	1832	1221	1382	1300	1221	1671	1382	1832
Cotingidae	*Pipreola arcuata*	1821	3650	1821	4018	4172	2189	2343	3650	2189	4018	2343	4172
Cotingidae	*Pipreola frontalis*	1000	1780	1000	2151	2305	1371	1525	1780	1371	2151	1525	2305
Cotingidae	*Pipreola intermedia*	1459	3101	1459	3473	3623	1831	1981	3101	1831	3473	1981	3623
Cotingidae	*Porphyrolaema porphyrolaema*	250	450	250	852	1029	652	829	450	652	852	829	1029
Cotingidae	*Querula purpurata*	250	1050	250	1436	1603	636	803	1050	636	1436	803	1603
Cotingidae	*Rupicola peruvianus*	650	2800	650	3172	3321	1022	1171	2800	1022	3172	1171	3321
Cotingidae	*Snowornis subalaris*	850	1350	850	1721	1882	1221	1382	1350	1221	1721	1382	1882
Cotingidae	*Tityra cayana*	250	450	250	852	1029	652	829	450	652	852	829	1029
Cotingidae	*Tityra inquisitor*	250	670	250	1064	1233	644	813	670	644	1064	813	1233
Cotingidae	*Tityra semifasciata*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Cracidae	*Aburria aburri*	650	1948	650	2319	2473	1021	1175	1948	1021	2319	1175	2473
Cracidae	*Mitu tuberosum*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Cracidae	*Ortalis guttata*	250	1600	250	1983	2144	633	794	1600	633	1983	794	2144
Cracidae	*Penelope jacquacu*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Cracidae	*Penelope montagnii*	900	3200	900	3572	3724	1272	1424	3200	1272	3572	1424	3724
Cracidae	*Pipile cumanensis*	250	500	250	894	1063	644	813	500	644	894	813	1063
Icteridae	*Cacicus cela*	250	1050	250	1436	1603	636	803	1050	636	1436	803	1603
Icteridae	*Cacicus chrysonotus*	2010	3342	2010	3714	3868	2382	2536	3342	2382	3714	2536	3868
Icteridae	*Cacicus haemorrhous*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Icteridae	*Clypicterus oseryi*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Icteridae	*Icterus icterus*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Icteridae	*Molothrus oryzivorus*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Icteridae	*Psarocolius angustifrons*	250	2083	250	2464	2622	631	789	2083	631	2464	789	2622
Icteridae	*Psarocolius atrovirens*	983	2750	983	3122	3271	1355	1504	2750	1355	3122	1504	3271
Icteridae	*Psarocolius bifasciatus*	250	970	250	1364	1533	644	813	970	644	1364	813	1533
Icteridae	*Psarocolius decumanus*	250	1320	250	1706	1873	636	803	1320	636	1706	803	1873
Odontophoridae	*Odontophorus balliviani*	800	3100	800	3472	3624	1172	1324	3100	1172	3472	1324	3624
Odontophoridae	*Odontophorus speciosus*	1000	2100	1000	2472	2622	1372	1522	2100	1372	2472	1522	2622
Odontophoridae	*Odontophorus stellatus*	250	1050	250	1436	1603	636	803	1050	636	1436	803	1603

Picidae	*Celeus elegans*	250	500	250	894	1063	644	813	500	644	894	813	1063
Picidae	*Celeus flavus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Picidae	*Celeus grammicus*	250	1200	250	1586	1753	636	803	1200	636	1586	803	1753
Picidae	*Celeus spectabilis*	250	500	250	894	1063	644	813	500	644	894	813	1063
Picidae	*Celeus torquatus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Picidae	*Colaptes rubiginosus*	750	2010	750	2382	2532	1122	1272	2010	1122	2382	1272	2532
Pipridae	*Chiroxiphia boliviana*	950	2033	950	2405	2555	1322	1472	2033	1322	2405	1472	2555
Pipridae	*Chiroxiphia pareola*	250	700	250	1094	1263	644	813	700	644	1094	813	1263
Pipridae	*Lepidothrix coeruleocapilla*	797	1709	797	2080	2234	1168	1322	1709	1168	2080	1322	2234
Pipridae	*Lepidothrix coronata*	250	900	250	1294	1463	644	813	900	644	1294	813	1463
Pipridae	*Machaeropterus pyrocephalus*	250	1429	250	1815	1982	636	803	1429	636	1815	803	1982
Pipridae	*Manacus manacus*	450	975	450	1362	1523	837	998	975	837	1362	998	1523
Pipridae	*Neopelma sulphureiventer*	250	500	250	894	1063	644	813	500	644	894	813	1063
Pipridae	*Pipra chloromeros*	250	1400	250	1786	1953	636	803	1400	636	1786	803	1953
Pipridae	*Pipra fasciicauda*	250	1055	250	1441	1608	636	803	1055	636	1441	803	1608
Pipridae	*Xenopipo holochlora*	450	1100	450	1479	1640	829	990	1100	829	1479	990	1640
Pipridae	*Xenopipo unicolor*	1000	1800	1000	2171	2325	1371	1525	1800	1371	2171	1525	2325
Psittacidae	*Amazona farinosa*	250	1350	250	1736	1903	636	803	1350	636	1736	803	1903
Psittacidae	*Amazona mercenaria*	826	3100	826	3472	3624	1198	1350	3100	1198	3472	1350	3624
Psittacidae	*Amazona ochrocephala*	250	850	250	1244	1413	644	813	850	644	1244	813	1413
Psittacidae	*Ara ararauna*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Psittacidae	*Ara chloropterus*	250	1390	250	1776	1943	636	803	1390	636	1776	803	1943
Psittacidae	*Ara macao*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Psittacidae	*Ara militaris*	600	1716	600	2087	2241	971	1125	1716	971	2087	1125	2241
Psittacidae	*Ara severus*	250	1236	250	1622	1789	636	803	1236	636	1622	803	1789
Psittacidae	*Aratinga leucophthalma*	250	1650	250	2033	2194	633	794	1650	633	2033	794	2194
Psittacidae	*Aratinga mitrata*	1621	3414	1621	3786	3937	1993	2144	3414	1993	3786	2144	3937
Psittacidae	*Aratinga weddellii*	250	700	250	1094	1263	644	813	700	644	1094	813	1263
Psittacidae	*Bolborhynchus lineola*	1100	3383	1100	3755	3905	1472	1622	3383	1472	3755	1622	3905
Psittacidae	*Bolborhynchus orbygnesius*	2500	3500	2500	3867	4023	2867	3023	3500	2867	3867	3023	4023
Psittacidae	*Brotogeris cyanoptera*	250	500	250	894	1063	644	813	500	644	894	813	1063
Psittacidae	*Brotogeris sanctithomae*	250	500	250	894	1063	644	813	500	644	894	813	1063
Psittacidae	*Forpus modestus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Psittacidae	*Nannopsittaca dachilleae*	250	1088	250	1474	1641	636	803	1088	636	1474	803	1641
Psittacidae	*Orthopsittaca manilata*	250	650	250	1044	1213	644	813	650	644	1044	813	1213
Psittacidae	*Pionites leucogaster*	250	500	250	894	1063	644	813	500	644	894	813	1063
Psittacidae	*Pionus menstruus*	250	2383	250	2764	2922	631	789	2383	631	2764	789	2922
Psittacidae	*Pionus tumultuosus*	1100	3032	1100	3404	3554	1472	1622	3032	1472	3404	1622	3554
Psittacidae	*Primolius couloni*	250	1300	250	1686	1853	636	803	1300	636	1686	803	1853
Psittacidae	*Pyrilia barrabandi*	250	500	250	894	1063	644	813	500	644	894	813	1063
Psittacidae	*Pyrrhura roseifrons*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Psittacidae	*Pyrrhura rupicola*	250	1100	250	1486	1653	636	803	1100	636	1486	803	1653
Psittacidae	*Touit huetii*	300	1300	300	1679	1840	679	840	1300	679	1679	840	1840
Psophiidae	*Psophia leucoptera*	250	1050	250	1436	1603	636	803	1050	636	1436	803	1603
Ramphastidae	*Andigena hypoglauca*	1450	3500	1450	3869	4021	1819	1971	3500	1819	3869	1971	4021
Ramphastidae	*Aulacorhynchus coeruleicinctis*	1059	2937	1059	3309	3455	1431	1577	2937	1431	3309	1577	3455
Ramphastidae	*Aulacorhynchus derbianus*	800	1852	800	2223	2377	1171	1325	1852	1171	2223	1325	2377
Ramphastidae	*Aulacorhynchus prasinus*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Ramphastidae	*Capito auratus*	250	1350	250	1736	1903	636	803	1350	636	1736	803	1903
Ramphastidae	*Eubucco richardsoni*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Ramphastidae	*Eubucco tucinkae*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Ramphastidae	*Eubucco versicolor*	750	2130	750	2502	2652	1122	1272	2130	1122	2502	1272	2652
Ramphastidae	*Pteroglossus azara*	250	1200	250	1586	1753	636	803	1200	636	1586	803	1753
Ramphastidae	*Pteroglossus beauharnaesii*	250	951	250	1345	1514	644	813	951	644	1345	813	1514
Ramphastidae	*Pteroglossus castanotis*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Ramphastidae	*Pteroglossus inscriptus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Ramphastidae	*Ramphastos tucanus*	250	876	250	1270	1439	644	813	876	644	1270	813	1439
Ramphastidae	*Ramphastos vitellinus*	250	600	250	994	1163	644	813	600	644	994	813	1163
Ramphastidae	*Selenidera reinwardtii*	250	1682	250	2065	2226	633	794	1682	633	2065	794	2226
Steatornithidae	*Steatornis caripensis*	450	900	450	1287	1448	837	998	900	837	1287	998	1448
Thraupidae	*Anisognathus igniventris*	2525	3600	2525	3964	4126	2889	3051	3600	2889	3964	3051	4126
Thraupidae	*Anisognathus somptuosus*	1375	3000	1375	3372	3522	1747	1897	3000	1747	3372	1897	3522
Thraupidae	*Buthraupis montana*	2312	3250	2312	3622	3776	2684	2838	3250	2684	3622	2838	3776
Thraupidae	*Catamblyrhynchus diadema*	2000	3250	2000	3622	3773	2372	2523	3250	2372	3622	2523	3773
Thraupidae	*Chlorochrysa calliparaea*	1000	2200	1000	2572	2722	1372	1522	2200	1372	2572	1522	2722
Thraupidae	*Chlorophanes spiza*	250	1430	250	1816	1983	636	803	1430	636	1816	803	1983
Thraupidae	*Chlorophonia cyanea*	250	2115	250	2496	2654	631	789	2115	631	2496	789	2654
Thraupidae	*Chlorornis riefferii*	2100	3215	2100	3587	3741	2472	2626	3215	2472	3587	2626	3741
Thraupidae	*Chlorospingus canigularis*	1000	1600	1000	1971	2125	1371	1525	1600	1371	1971	1525	2125

Thraupidae	*Chlorospingus flavigularis*	800	2350	800	2722	2872	1172	1322	2350	1172	2722	1322	2872
Thraupidae	*Chlorospingus ophthalmicus*	1000	2561	1000	2933	3082	1372	1521	2561	1372	2933	1521	3082
Thraupidae	*Chlorospingus parvirostris*	1100	2600	1100	2972	3118	1472	1618	2600	1472	2972	1618	3118
Thraupidae	*Cissopis leverianus*	250	1600	250	1983	2144	633	794	1600	633	1983	794	2144
Thraupidae	*Conirostrum cinereum*	2850	3500	2850	3864	4026	3214	3376	3500	3214	3864	3376	4026
Thraupidae	*Conirostrum speciosum*	250	900	250	1294	1463	644	813	900	644	1294	813	1463
Thraupidae	*Cyanerpes caeruleus*	250	1400	250	1786	1953	636	803	1400	636	1786	803	1953
Thraupidae	*Cyanerpes cyaneus*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Thraupidae	*Dacnis cayana*	250	1550	250	1933	2094	633	794	1550	633	1933	794	2094
Thraupidae	*Dacnis flaviventer*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Thraupidae	*Dacnis lineata*	250	1300	250	1686	1853	636	803	1300	636	1686	803	1853
Thraupidae	*Delothraupis castaneoventris*	2305	3520	2305	3887	4043	2672	2828	3520	2672	3887	2828	4043
Thraupidae	*Diglossa brunneiventris*	2518	3560	2518	3924	4086	2882	3044	3560	2882	3924	3044	4086
Thraupidae	*Diglossa caerulescens*	1399	2700	1399	3072	3218	1771	1917	2700	1771	3072	1917	3218
Thraupidae	*Diglossa cyanea*	1394	3600	1394	3969	4121	1763	1915	3600	1763	3969	1915	4121
Thraupidae	*Diglossa glauca*	1000	2300	1000	2672	2822	1372	1522	2300	1372	2672	1522	2822
Thraupidae	*Diglossa mystacalis*	2600	3600	2600	3964	4126	2964	3126	3600	2964	3964	3126	4126
Thraupidae	*Diglossa sittoides*	1900	3600	1900	3968	4122	2268	2422	3600	2268	3968	2422	4122
Thraupidae	*Dubusia taeniata*	1900	3200	1900	3572	3723	2272	2423	3200	2272	3572	2423	3723
Thraupidae	*Euphonia chlorotica*	250	450	250	852	1029	652	829	450	652	852	829	1029
Thraupidae	*Euphonia chrysopasta*	250	950	250	1344	1513	644	813	950	644	1344	813	1513
Thraupidae	*Euphonia laniirostris*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Thraupidae	*Euphonia mesochrysa*	600	1800	600	2171	2325	971	1125	1800	971	2171	1125	2325
Thraupidae	*Euphonia minuta*	250	1050	250	1436	1603	636	803	1050	636	1436	803	1603
Thraupidae	*Euphonia rufiventris*	250	950	250	1344	1513	644	813	950	644	1344	813	1513
Thraupidae	*Euphonia xanthogaster*	250	2130	250	2511	2669	631	789	2130	631	2511	789	2669
Thraupidae	*Iridophanes pulcherrimus*	1100	1800	1100	2172	2318	1472	1618	1800	1472	2172	1618	2318
Thraupidae	*Iridosornis analis*	1000	2200	1000	2572	2722	1372	1522	2200	1372	2572	1522	2722
Thraupidae	*Iridosornis jelskii*	2200	3500	2200	3867	4023	2567	2723	3500	2567	3867	2723	4023
Thraupidae	*Lamprospiza melanoleuca*	250	900	250	1294	1463	644	813	900	644	1294	813	1463
Thraupidae	*Pipraeidea melanonota*	450	3000	450	3374	3528	824	978	3000	824	3374	978	3528
Thraupidae	*Piranga leucoptera*	900	1800	900	2171	2325	1271	1425	1800	1271	2171	1425	2325
Thraupidae	*Piranga rubra*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Thraupidae	*Ramphocelus carbo*	250	1600	250	1983	2144	633	794	1600	633	1983	794	2144
Thraupidae	*Ramphocelus nigrogularis*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Thraupidae	*Schistochlamys melanopis*	600	2600	600	2972	3121	972	1121	2600	972	2972	1121	3121
Thraupidae	*Tachyphonus cristatus*	300	450	300	852	1029	702	879	450	702	852	879	1029
Thraupidae	*Tachyphonus rufiventer*	250	1250	250	1636	1803	636	803	1250	636	1636	803	1803
Thraupidae	*Tangara arthus*	600	1800	600	2171	2325	971	1125	1800	971	2171	1125	2325
Thraupidae	*Tangara callophrys*	250	950	250	1344	1513	644	813	950	644	1344	813	1513
Thraupidae	*Tangara chilensis*	250	1921	250	2304	2465	633	794	1921	633	2304	794	2465
Thraupidae	*Tangara chrysotis*	850	2115	850	2487	2637	1222	1372	2115	1222	2487	1372	2637
Thraupidae	*Tangara cyanicollis*	500	2000	500	2375	2529	875	1029	2000	875	2375	1029	2529
Thraupidae	*Tangara cyanotis*	1300	2000	1300	2372	2518	1672	1818	2000	1672	2372	1818	2518
Thraupidae	*Tangara gyrola*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Thraupidae	*Tangara mexicana*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Thraupidae	*Tangara nigrocincta*	250	1100	250	1486	1653	636	803	1100	636	1486	803	1653
Thraupidae	*Tangara nigroviridis*	1220	2500	1220	2872	3018	1592	1738	2500	1592	2872	1738	3018
Thraupidae	*Tangara parzudakii*	1375	2000	1375	2372	2518	1747	1893	2000	1747	2372	1893	2518
Thraupidae	*Tangara punctata*	600	2000	600	2372	2522	972	1122	2000	972	2372	1122	2522
Thraupidae	*Tangara ruficervix*	1000	2100	1000	2472	2622	1372	1522	2100	1372	2472	1522	2622
Thraupidae	*Tangara schrankii*	250	1100	250	1486	1653	636	803	1100	636	1486	803	1653
Thraupidae	*Tangara vassorii*	1690	3250	1690	3622	3773	2062	2213	3250	2062	3622	2213	3773
Thraupidae	*Tangara velia*	250	600	250	994	1163	644	813	600	644	994	813	1163
Thraupidae	*Tangara viridicollis*	800	2600	800	2972	3121	1172	1321	2600	1172	2972	1321	3121
Thraupidae	*Tangara xanthocephala*	1000	2500	1000	2872	3021	1372	1521	2500	1372	2872	1521	3021
Thraupidae	*Tangara xanthogastra*	250	1400	250	1786	1953	636	803	1400	636	1786	803	1953
Thraupidae	*Tersina viridis*	250	1450	250	1836	2003	636	803	1450	636	1836	803	2003
Thraupidae	*Thlypopsis sordida*	250	600	250	994	1163	644	813	600	644	994	813	1163
Thraupidae	*Thraupis bonariensis*	1000	3500	1000	3869	4023	1369	1523	3500	1369	3869	1523	4023
Thraupidae	*Thraupis cyanocephala*	1335	3032	1335	3404	3554	1707	1857	3032	1707	3404	1857	3554
Thraupidae	*Thraupis episcopus*	250	1600	250	1983	2144	633	794	1600	633	1983	794	2144
Thraupidae	*Thraupis palmarum*	250	1600	250	1983	2144	633	794	1600	633	1983	794	2144
Thraupidae	*Trichothraupis melanops*	1000	1650	1000	2021	2175	1371	1525	1650	1371	2021	1525	2175
Tinamidae	*Crypturellus atrocapillus*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Tinamidae	*Crypturellus bartletti*	250	500	250	894	1063	644	813	500	644	894	813	1063
Tinamidae	*Crypturellus cinereus*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Tinamidae	*Crypturellus obsoletus*	450	3013	450	3387	3541	824	978	3013	824	3387	978	3541
Tinamidae	*Crypturellus soui*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044

Tinamidae	*Crypturellus strigulosus*	350	750	350	1137	1298	737	898	750	737	1137	898	1298
Tinamidae	*Crypturellus undulatus*	250	800	250	1194	1363	644	813	800	644	1194	813	1363
Tinamidae	*Crypturellus variegatus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Tinamidae	*Nothocercus nigrocapillus*	1600	3200	1600	3572	3723	1972	2123	3200	1972	3572	2123	3723
Tinamidae	*Tinamus guttatus*	250	1100	250	1486	1653	636	803	1100	636	1486	803	1653
Tinamidae	*Tinamus major*	250	700	250	1094	1263	644	813	700	644	1094	813	1263
Tinamidae	*Tinamus tao*	250	1300	250	1686	1853	636	803	1300	636	1686	803	1853
Trogonidae	*Pharomachrus antisianus*	1000	2338	1000	2710	2860	1372	1522	2338	1372	2710	1522	2860
Trogonidae	*Pharomachrus auriceps*	1300	3049	1300	3421	3571	1672	1822	3049	1672	3421	1822	3571
Trogonidae	*Pharomachrus pavoninus*	250	1200	250	1586	1753	636	803	1200	636	1586	803	1753
Trogonidae	*Trogon collaris*	250	1489	250	1875	2042	636	803	1489	636	1875	803	2042
Trogonidae	*Trogon curucui*	250	1500	250	1883	2044	633	794	1500	633	1883	794	2044
Trogonidae	*Trogon melanurus*	250	1000	250	1386	1553	636	803	1000	636	1386	803	1553
Trogonidae	*Trogon personatus*	1100	3500	1100	3869	4021	1469	1621	3500	1469	3869	1621	4021
Trogonidae	*Trogon violaceus*	250	876	250	1270	1439	644	813	876	644	1270	813	1439
Trogonidae	*Trogon viridis*	250	878	250	1272	1441	644	813	878	644	1272	813	1441
Turdidae	*Catharus fuscater*	1500	2850	1500	3222	3368	1872	2018	2850	1872	3222	2018	3368
Turdidae	*Catharus ustulatus*	250	3500	250	3876	4033	626	783	3500	626	3876	783	4033
Turdidae	*Entomodestes leucotis*	1139	2900	1139	3272	3418	1511	1657	2900	1511	3272	1657	3418
Turdidae	*Myadestes ralloides*	750	2900	750	3272	3421	1122	1271	2900	1122	3272	1271	3421
Turdidae	*Turdus albicollis*	250	850	250	1244	1413	644	813	850	644	1244	813	1413
Turdidae	*Turdus amaurochalinus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Turdidae	*Turdus chiguanco*	1300	3520	1300	3889	4041	1669	1821	3520	1669	3889	1821	4041
Turdidae	*Turdus fuscater*	2500	3500	2500	3867	4023	2867	3023	3500	2867	3867	3023	4023
Turdidae	*Turdus hauxwelli*	250	1496	250	1882	2049	636	803	1496	636	1882	803	2049
Turdidae	*Turdus ignobilis*	250	1640	250	2023	2184	633	794	1640	633	2023	794	2184
Turdidae	*Turdus leucops*	850	2600	850	2972	3121	1222	1371	2600	1222	2972	1371	3121
Turdidae	*Turdus nigriceps*	250	1851	250	2234	2395	633	794	1851	633	2234	794	2395
Turdidae	*Turdus serranus*	1400	3342	1400	3714	3864	1772	1922	3342	1772	3714	1922	3864
Tyrannidae	*Elaenia albiceps*	500	3250	500	3624	3778	874	1028	3250	874	3624	1028	3778
Tyrannidae	*Elaenia flavogaster*	450	900	450	1287	1448	837	998	900	837	1287	998	1448
Tyrannidae	*Elaenia gigas*	250	1550	250	1933	2094	633	794	1550	633	1933	794	2094
Tyrannidae	*Elaenia obscura*	1700	3000	1700	3372	3523	2072	2223	3000	2072	3372	2223	3523
Tyrannidae	*Elaenia pallatangae*	1100	3250	1100	3622	3772	1472	1622	3250	1472	3622	1622	3772
Tyrannidae	*Elaenia parvirostris*	250	1300	250	1686	1853	636	803	1300	636	1686	803	1853
Tyrannidae	*Elaenia spectabilis*	250	1450	250	1836	2003	636	803	1450	636	1836	803	2003
Tyrannidae	*Elaenia strepera*	250	450	250	852	1029	652	829	450	652	852	829	1029
Tyrannidae	*Lophotriccus pileatus*	800	1821	800	2192	2346	1171	1325	1821	1171	2192	1325	2346
Tyrannidae	*Mionectes macconnelli*	250	1200	250	1586	1753	636	803	1200	636	1586	803	1753
Tyrannidae	*Mionectes oleagineus*	250	1350	250	1736	1903	636	803	1350	636	1736	803	1903
Tyrannidae	*Mionectes olivaceus*	250	1712	250	2095	2256	633	794	1712	633	2095	794	2256
Tyrannidae	*Mionectes striaticollis*	550	3377	550	3749	3901	922	1074	3377	922	3749	1074	3901
Tyrannidae	*Tyrannus savana*	250	500	250	894	1063	644	813	500	644	894	813	1063
Tyrannidae	*Tyrannus tyrannus*	250	500	250	894	1063	644	813	500	644	894	813	1063
Tyrannidae	*Zimmerius bolivianus*	1000	2901	1000	3273	3422	1372	1521	2901	1372	3273	1521	3422
Tyrannidae	*Zimmerius gracilipes*	250	850	250	1244	1413	644	813	850	644	1244	813	1413

Table S4.2. Current and future probabilities of occurrence derived from SDMs of all 240 frugivorous bird species of the Manú Biosphere Reserve, Peru, based on the MIROC5 climate model. SDM models were based on current and future local temperature and precipitation values. (“cur” = current, “6.0” = RCP 6.0, ”8.5” = RCP 8.5)

		500 m			1000 m			1500 m			2000 m			2500 m			3000 m			3500 m		
Family	Bird species	cur	6.0	8.5	cur	6.0	8.5	cur	6.0	8.5	cur	6.0	8.5	cur	6.0	8.5	cur	6.0	8.5	cur	6.0	8.5
Cardinalidae	*Cyanocompsa cyanoides*	0.354	0.936	0.980	0.965	0.975	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardinalidae	*Pheucticus aureoventris*	0	0	0	0.302	0.027	0.597	0.008	0.183	0.163	0.028	0.321	0.232	0.007	0.013	0.008	0.043	0.007	0.063	0	0	0
Cardinalidae	*Pheucticus chrysogaster*	0	0	0	0.063	0.011	0.215	0.476	0.179	0.005	0.520	0.054	0.036	0.004	0.052	0.244	0.004	0.064	0.605	0.010	0.004	0.004
Cardinalidae	*Saltator aurantiirostris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0.002	0.002	0.003	0.004	0.004
Cardinalidae	*Saltator coerulescens*	0.023	0.013	0.072	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardinalidae	*Saltator grossus*	0.195	0.553	0.886	0.988	0.841	0.976	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardinalidae	*Saltator maximus*	0.514	0.452	0.729	0.903	0.424	0.962	0.136	0.958	0.955	0.941	0.634	0.756	0.007	0.168	0.705	0	0	0	0	0	0
Columbidae	*Geotrygon montana*	0.731	0.286	0.893	0.270	0.567	0.880	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Columbidae	*Patagioenas cayennensis*	0.067	0.013	0.730	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Columbidae	*Patagioenas fasciata*	0	0	0	0	0	0	0.790	0.496	0.167	0.993	0.899	0.326	0.969	0.796	0.899	0.090	0.296	0.457	0.005	0.170	0.004
Columbidae	*Patagioenas plumbea*	0.075	0.188	0.088	0.344	0.272	0.768	0.030	0.978	0.991	0	0	0	0	0	0	0	0	0	0	0	0
Columbidae	*Patagioenas subvinacea*	0.008	0.020	0.136	0.593	0.955	0.980	0.698	0.792	0.967	0	0	0	0	0	0	0	0	0	0	0	0
Corvidae	*Cyanocorax cyanomelas*	0.338	0.004	0.004	0.496	0.701	0.972	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corvidae	*Cyanocorax violaceus*	0.544	0.005	0.278	0.207	0.971	0.991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corvidae	*Cyanocorax yncas*	0	0	0	0	0	0	0.453	0.402	0.035	0.994	0.992	0.776	0	0	0	0	0	0	0	0	0
Cotingidae	*Ampelioides tschudii*	0	0	0	0.765	0.977	0.790	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Ampelion rubrocristatus*	0	0	0	0	0	0	0	0	0	0	0	0	0.903	0.939	0.255	0.015	0.291	0.453	0	0	0
Cotingidae	*Ampelion rufaxilla*	0	0	0	0	0	0	0	0	0	0.427	0.078	0.191	0.400	0.432	0.539	0	0	0	0	0	0
Cotingidae	*Cephalopterus ornatus*	0.371	0.175	0.659	0.044	0.842	0.935	0.534	0.792	0.681	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Conioptilon mcilhennyi*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Cotinga cayana*	0.818	0.076	0.048	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Cotinga maynana*	0.023	0.003	0	0.271	0.962	0.994	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Gymnoderus foetidus*	0.010	0.010	0.230	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Iodopleura isabellae*	0.842	0.116	0.375	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Laniocera hypopyrra*	0.049	0.285	0.118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Lipaugus vociferans*	0.041	0.009	0.012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Oxyruncus cristatus*	0	0	0	0.804	0.837	0.776	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Pipreola arcuata*	0	0	0	0	0	0	0	0	0	0.906	0.043	0.022	0.612	0.915	0.999	0.356	0.932	0.965	0.189	0.992	0.193
Cotingidae	*Pipreola frontalis*	0	0	0	0.990	0.667	0.779	0.950	0.948	0.544	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Pipreola intermedia*	0	0	0	0	0	0	0.036	0.010	0.010	0.054	0.030	0.007	0.095	0.037	0.051	0.302	0.969	0.988	0	0	0
Cotingidae	*Porphyrolaema porphyrolaema*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Querula purpurata*	0.021	0.030	0.011	0.436	0.932	0.944	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Rupicola peruvianus*	0	0	0	0.996	0.766	0.311	0.995	0.998	0.930	0.909	0.988	0.995	0.733	0.946	0.998	0	0	0	0	0	0
Cotingidae	*Snowornis subalaris*	0	0	0	0.961	0.973	0.987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Tityra cayana*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Tityra inquisitor*	0.856	0.061	0.462	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingidae	*Tityra semifasciata*	0.424	0.600	0.867	0.967	0.968	0.976	0.984	0.913	0.990	0	0	0	0	0	0	0	0	0	0	0	0
Cracidae	*Aburria aburri*	0	0	0	0.985	0.988	0.996	0.995	0.999	0.931	0	0	0	0	0	0	0	0	0	0	0	0

Cracidae	*Mitu tuberosum*	0.903	0.034	0.336	0.044	0.972	0.993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cracidae	*Ortalis guttata*	0.577	0.006	0.020	0.978	0.769	0.649	0.136	0.968	0.990	0	0	0	0	0	0	0	0	0	0	0	0
Cracidae	*Penelope jacquacu*	0.078	0.006	0.022	0.139	0.130	0.988	0.004	0.337	0.821	0	0	0	0	0	0	0	0	0	0	0	0
Cracidae	*Penelope montagnii*	0	0	0	0.224	0.014	0.008	0.109	0.123	0.588	0.491	0.686	0.036	0.624	0.877	0.982	0.151	0.705	0.906	0	0	0
Cracidae	*Pipile cumanensis*	0.113	0.012	0.024	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Cacicus cela*	0.789	0.023	0.071	0.008	0.700	0.868	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Cacicus chrysonotus*	0	0	0	0	0	0	0	0	0	0	0	0	0.874	0.957	0.996	0.295	0.058	0.084	0	0	0
Icteridae	*Cacicus haemorrhous*	0.006	0.206	0.040	0.007	0.022	0.041	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Clypicterus oseryi*	0.988	0.058	0.026	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Icterus icterus*	0.074	0.028	0.484	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Molothrus oryzivorus*	0.216	0.115	0.059	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Psarocolius angustifrons*	0.244	0.009	0.005	0.493	0.813	0.981	0.073	0.784	0.943	0.707	0.954	0.954	0	0	0	0	0	0	0	0	0
Icteridae	*Psarocolius atrovirens*	0	0	0	0.699	0.707	0.012	0.775	0.981	0.546	0.551	0.922	0.982	0.009	0.208	0.222	0	0	0	0	0	0
Icteridae	*Psarocolius bifasciatus*	0.932	0.066	0.483	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icteridae	*Psarocolius decumanus*	0.892	0.499	0.262	0.978	0.653	0.786	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odontophoridae	*Odontophorus balliviani*	0	0	0	0.148	0.030	0.005	0.956	0.065	0.090	0.955	0.420	0.062	0.475	0.631	0.406	0.411	0.568	0.658	0	0	0
Odontophoridae	*Odontophorus speciosus*	0	0	0	0.981	0.064	0.031	0.828	0.986	0.981	0.418	0.968	0.988	0	0	0	0	0	0	0	0	0
Odontophoridae	*Odontophorus stellatus*	0.016	0.008	0.003	0.253	0.431	0.998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picidae	*Celeus elegans*	0.264	0.337	0.400	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picidae	*Celeus flavus*	0.201	0.173	0.158	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picidae	*Celeus grammicus*	0.791	0.621	0.408	0.030	0.138	0.993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picidae	*Celeus spectabilis*	0.201	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picidae	*Celeus torquatus*	0.190	0.152	0.226	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picidae	*Colaptes rubiginosus*	0	0	0	0.985	0.804	0.603	0.995	0.978	0.980	0.986	0.821	0.950	0	0	0	0	0	0	0	0	0
Pipridae	*Chiroxiphia boliviana*	0	0	0	0.142	0.121	0.135	0.123	0.883	0.905	0.028	0.198	0.881	0	0	0	0	0	0	0	0	0
Pipridae	*Chiroxiphia pareola*	0.463	0.236	0.150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Lepidothrix coeruleocapilla*	0	0	0	0.972	0.448	0.556	0.044	0.993	0.984	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Lepidothrix coronata*	0.825	0.579	0.187	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Machaeropterus pyrocephalus*	0.074	0.005	0.004	0.240	0.984	0.986	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Manacus manacus*	0.895	0.495	0.951	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Neopelma sulphureiventer*	0.311	0.137	0.083	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Pipra chloromeros*	0.409	0.013	0.013	0.851	0.925	0.762	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Pipra fasciicauda*	0.005	0.003	0.003	0.413	0.804	0.985	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Xenopipo holochlora*	0.983	0.262	0.262	0.799	0.990	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pipridae	*Xenopipo unicolor*	0	0	0	0.415	0.114	0.031	0.236	0.466	0.449	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Amazona farinosa*	0.033	0.071	0.573	0.034	0.302	0.987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Amazona mercenaria*	0	0	0	0.974	0.659	0.511	0.974	0.970	0.811	0.977	0.976	0.973	0.981	0.981	0.980	0.948	0.759	0.809	0	0	0
Psittacidae	*Amazona ochrocephala*	0.009	0.018	0.314	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Ara ararauna*	0.512	0.107	0.115	0.022	0.322	0.880	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Ara chloropterus*	0.079	0.033	0.194	0.004	0.063	0.847	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Ara macao*	0.007	0.020	0.022	0.070	0.035	0.127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Ara militaris*	0	0	0	0.978	0.938	0.884	0.971	0.975	0.974	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Ara severus*	0.114	0.712	0.945	0.120	0.102	0.990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Aratinga leucophthalma*	0.019	0.011	0.011	0.021	0.181	0.832	0.006	0.149	0.165	0	0	0	0	0	0	0	0	0	0	0	0

Psittacidae	*Aratinga mitrata*	0	0	0	0	0	0	0	0	0	0.001	0.008	0.003	0.002	0.002	0.001	0.002	0.002	0.005	0	0	0
Psittacidae	*Aratinga weddellii*	0.179	0.015	0.003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Bolborhynchus lineola*	0	0	0	0	0	0	0.961	0.850	0.757	0.968	0.919	0.821	0.658	0.977	0.975	0.110	0.966	0.975	0	0	0
Psittacidae	*Bolborhynchus orbygnesius*	0	0	0	0	0	0	0	0	0	0	0	0	0.076	0.067	0.048	0.348	0.143	0.199	0.110	0.215	0.233
Psittacidae	*Brotogeris cyanoptera*	0.052	0.007	0.147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Brotogeris sanctithomae*	0.064	0.008	0.011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Forpus modestus*	0.017	0.017	0.017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Nannopsittaca dachilleae*	0.973	0.814	0.814	0.044	0.374	0.496	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Orthopsittaca manilata*	0.098	0.007	0.007	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Pionites leucogaster*	0.004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Pionus menstruus*	0.137	0.161	0.542	0.489	0.518	0.981	0.078	0.546	0.762	0.653	0.039	0.050	0	0	0	0	0	0	0	0	0
Psittacidae	*Pionus tumultuosus*	0	0	0	0	0	0	0.959	0.029	0.418	0.989	0.076	0.024	0.893	0.990	0.993	0.297	0.990	0.991	0	0	0
Psittacidae	*Primolius couloni*	0.109	0.006	0.006	0.050	0.975	0.991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Pyrilia barrabandi*	0.010	0.210	0.689	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Pyrrhura roseifrons*	0.956	0.230	0.267	0.006	0.749	0.975	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Pyrrhura rupicola*	0.154	0.004	0.004	0.141	0.207	0.662	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	*Touit huetii*	0.264	0.318	0.062	0.005	0.018	0.941	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psophiidae	*Psophia leucoptera*	0.995	0.274	0.159	0.057	0.563	0.996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Andigena hypoglauca*	0	0	0	0	0	0	0.017	0.003	0.003	0.008	0.003	0.003	0.230	0.047	0.026	0.767	0.928	0.688	0.814	0.200	0.147
Ramphastidae	*Aulacorhynchus coeruleicinctis*	0	0	0	0	0	0	0.915	0.871	0.635	0.707	0.928	0.863	0.043	0.671	0.520	0	0	0	0	0	0
Ramphastidae	*Aulacorhynchus derbianus*	0	0	0	0.984	0.984	0.982	0.705	0.981	0.983	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Aulacorhynchus prasinus*	0.116	0.001	0.001	0.937	0.976	0.986	0.948	0.841	0.898	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Capito auratus*	0.079	0.008	0.012	0.018	0.143	0.880	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Eubucco richardsoni*	0.961	0.012	0.010	0.376	0.949	0.986	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Eubucco tucinkae*	0.602	0.073	0.073	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Eubucco versicolor*	0	0	0	0.909	0.167	0.003	0.063	0.849	0.924	0.004	0.753	0.570	0	0	0	0	0	0	0	0	0
Ramphastidae	*Pteroglossus azara*	0.887	0.075	0.093	0.034	0.976	0.971	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Pteroglossus beauharnaesii*	0.022	0.024	0.021	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Pteroglossus castanotis*	0.645	0.017	0.029	0.135	0.414	0.920	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Pteroglossus inscriptus*	0.384	0.037	0.023	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Ramphastos tucanus*	0.007	0.015	0.034	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Ramphastos vitellinus*	0.204	0.204	0.460	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastidae	*Selenidera reinwardtii*	0.909	0.084	0.005	0.154	0.686	0.849	0.001	0.064	0.835	0	0	0	0	0	0	0	0	0	0	0	0
Steatornithidae	*Steatornis caripensis*	0.992	0.056	0.264	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Anisognathus igniventris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.551	0.940	0.993	0.878	0.767	0.005
Thraupidae	*Anisognathus somptuosus*	0	0	0	0	0	0	0.684	0.871	0.045	0.998	0.414	0.543	0.130	0.831	0.894	0.051	0.009	0.400	0	0	0
Thraupidae	*Buthraupis montana*	0	0	0	0	0	0	0	0	0	0	0	0	0.370	0.864	0.990	0.040	0.232	0.807	0	0	0
Thraupidae	*Catamblyrhynchus diadema*	0	0	0	0	0	0	0	0	0	0.862	0.119	0.066	0.921	0.940	0.942	0.864	0.945	0.953	0	0	0
Thraupidae	*Chlorochrysa calliparaea*	0	0	0	0.876	0.745	0.967	0.585	0.925	0.819	0.988	0.119	0.614	0	0	0	0	0	0	0	0	0
Thraupidae	*Chlorophanes spiza*	0.924	0.501	0.319	0.960	0.930	0.966	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Chlorophonia cyanea*	0.051	0.004	0.004	0.913	0.339	0.199	0.993	0.904	0.978	0.335	0.900	0.890	0	0	0	0	0	0	0	0	0
Thraupidae	*Chlorornis riefferii*	0	0	0	0	0	0	0	0	0	0	0	0	0.813	0.884	0.995	0.561	0.991	0.993	0	0	0
Thraupidae	*Chlorospingus canigularis*	0	0	0	0.970	0.444	0.006	0.881	0.812	0.610	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Chlorospingus flavigularis*	0	0	0	0.985	0.662	0.666	0.995	0.992	0.996	0.985	0.994	0.994	0	0	0	0	0	0	0	0	0

Thraupidae	*Chlorospingus ophthalmicus*	0	0	0	0.974	0.358	0.212	0.129	0.289	0.122	0.166	0.209	0.206	0.776	0.919	0.993	0	0	0	0	0	0
Thraupidae	*Chlorospingus parvirostris*	0	0	0	0	0	0	0.194	0.910	0.872	0.754	0.699	0.838	0.096	0.855	0.984	0	0	0	0	0	0
Thraupidae	*Cissopis leverianus*	0.982	0.020	0.009	0.971	0.965	0.919	0.010	0.856	0.898	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Conirostrum cinereum*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	0.012	0.337	0.014	0.003	0.003
Thraupidae	*Conirostrum speciosum*	0.016	0.010	0.015	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Cyanerpes caeruleus*	0.868	0.111	0.693	0.665	0.579	0.928	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Cyanerpes cyaneus*	0.018	0.107	0.648	0.005	0.083	0.034	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Dacnis cayana*	0.952	0.736	0.347	0.840	0.838	0.179	0.093	0.216	0.969	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Dacnis flaviventer*	0.894	0.263	0.035	0.209	0.950	0.993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Dacnis lineata*	0.344	0.088	0.033	0.893	0.990	0.402	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Delothraupis castaneoventris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.004	0.070	0.080	0.039	0	0.007	0.003
Thraupidae	*Diglossa brunneiventris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003	0.006	0.001	0.007	0.063	0.044
Thraupidae	*Diglossa caerulescens*	0	0	0	0	0	0	0.041	0.992	0.132	0.021	0.860	0.622	0.977	0.997	0.998	0	0	0	0	0	0
Thraupidae	*Diglossa cyanea*	0	0	0	0	0	0	0.075	0.015	0.096	0.982	0.147	0.072	0.969	0.280	0.956	0.044	0.653	0.303	0.125	0.042	0.003
Thraupidae	*Diglossa glauca*	0	0	0	0.999	0.957	0.491	0.617	0.990	0.993	0.238	0.988	0.960	0	0	0	0	0	0	0	0	0
Thraupidae	*Diglossa mystacalis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.185	0.091	0.097	0.033	0.011	0.003
Thraupidae	*Diglossa sittoides*	0	0	0	0	0	0	0	0	0	0.967	0.921	0.700	0.216	0.711	0.375	0.062	0.682	0.779	0.004	0.005	0.004
Thraupidae	*Dubusia taeniata*	0	0	0	0	0	0	0	0	0	0.106	0.008	0.006	0.863	0.657	0.868	0.374	0.156	0.731	0	0	0
Thraupidae	*Euphonia chlorotica*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Euphonia chrysopasta*	0.882	0.062	0.074	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Euphonia laniirostris*	0.020	0.152	0.188	0.794	0.922	0.863	0.909	0.840	0.824	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Euphonia mesochrysa*	0	0	0	0.968	0.048	0.034	0.935	0.981	0.970	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Euphonia minuta*	0.484	0.434	0.073	0.122	0.879	0.971	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Euphonia rufiventris*	0.157	0.236	0.192	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Euphonia xanthogaster*	0.950	0.151	0.305	0.988	0.510	0.272	0.655	0.862	0.989	0.914	0.973	0.958	0	0	0	0	0	0	0	0	0
Thraupidae	*Iridophanes pulcherrimus*	0	0	0	0	0	0	0.984	0.232	0.396	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Iridosornis analis*	0	0	0	0.983	0.323	0.050	0.864	0.973	0.793	0.886	0.988	0.991	0	0	0	0	0	0	0	0	0
Thraupidae	*Iridosornis jelskii*	0	0	0	0	0	0	0	0	0	0	0	0	0.003	0.056	0.052	0.195	0.144	0.195	0.003	0.005	0.005
Thraupidae	*Lamprospiza melanoleuca*	0.286	0.042	0.457	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Pipraeidea melanonota*	0.441	0.003	0.003	0.510	0.073	0.629	0.310	0.625	0.325	0.480	0.681	0.784	0.273	0.790	0.991	0.007	0.677	0.929	0	0	0
Thraupidae	*Piranga leucoptera*	0	0	0	0.963	0.522	0.013	0.860	0.965	0.992	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Piranga rubra*	0.343	0.623	0.271	0.955	0.837	0.669	0.913	0.993	0.979	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Ramphocelus carbo*	0.188	0.017	0.132	0.366	0.343	0.636	0.103	0.053	0.398	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Ramphocelus nigrogularis*	0.867	0.037	0.023	0.039	0.722	0.969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Schistochlamys melanopis*	0	0	0	0.931	0.978	0.838	0.239	0.958	0.993	0.044	0.061	0.330	0.010	0.011	0.040	0	0	0	0	0	0
Thraupidae	*Tachyphonus cristatus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tachyphonus rufiventer*	0.676	0.052	0.028	0.982	0.993	0.993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara arthus*	0	0	0	0.985	0.884	0.388	0.636	0.832	0.972	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara callophrys*	0.830	0.011	0.011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara chilensis*	0.278	0.036	0.005	0.976	0.935	0.898	0.243	0.847	0.847	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara chrysotis*	0	0	0	0.986	0.984	0.232	0.779	0.441	0.993	0.154	0.928	0.295	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara cyanicollis*	0.548	0.006	0.248	0.988	0.731	0.762	0.749	0.782	0.953	0.724	0.993	0.977	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara cyanotis*	0	0	0	0	0	0	0.320	0.595	0.408	0.945	0.787	0.548	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara gyrola*	0.419	0.006	0.020	0.992	0.827	0.236	0.898	0.991	0.972	0	0	0	0	0	0	0	0	0	0	0	0

Thraupidae	*Tangara mexicana*	0.389	0.154	0.027	0.243	0.971	0.991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara nigrocincta*	0.978	0.066	0.069	0.564	0.950	0.998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara nigroviridis*	0	0	0	0	0	0	0.962	0.745	0.186	0.992	0.165	0.885	0.973	0.317	0.995	0	0	0	0	0	0
Thraupidae	*Tangara parzudakii*	0	0	0	0	0	0	0.995	0.625	0.139	0.991	0.732	0.318	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara punctata*	0	0	0	0.989	0.955	0.952	0.427	0.952	0.869	0.277	0.761	0.855	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara ruficervix*	0	0	0	0.978	0.084	0.013	0.987	0.636	0.421	0.991	0.136	0.197	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara schrankii*	0.203	0.025	0.003	0.231	0.742	0.969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara vassorii*	0	0	0	0	0	0	0	0	0	0.545	0.119	0.263	0.550	0.940	0.993	0.972	0.021	0.123	0	0	0
Thraupidae	*Tangara velia*	0.286	0.040	0.045	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tangara viridicollis*	0	0	0	0.066	0.002	0.002	0.023	0.196	0.004	0.133	0.077	0.297	0.005	0.002	0.002	0	0	0	0	0	0
Thraupidae	*Tangara xanthocephala*	0	0	0	0.871	0.797	0.003	0.459	0.958	0.285	0.974	0.167	0.790	0.908	0.987	0.998	0	0	0	0	0	0
Thraupidae	*Tangara xanthogastra*	0.583	0.055	0.045	0.926	0.979	0.992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Tersina viridis*	0.590	0.065	0.285	0.994	0.427	0.570	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Thlypopsis sordida*	0.741	0.123	0.057	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Thraupis bonariensis*	0	0	0	0.002	0.002	0.002	0.006	0.089	0.011	0.183	0.020	0.135	0.002	0.068	0.068	0.003	0.066	0.299	0.002	0.002	0.002
Thraupidae	*Thraupis cyanocephala*	0	0	0	0	0	0	0.794	0.263	0.005	0.938	0.743	0.149	0.934	0.885	0.674	0.142	0.107	0.023	0	0	0
Thraupidae	*Thraupis episcopus*	0.109	0.267	0.617	0.267	0.549	0.190	0.458	0.299	0.762	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Thraupis palmarum*	0.092	0.296	0.076	0.307	0.705	0.152	0.321	0.348	0.978	0	0	0	0	0	0	0	0	0	0	0	0
Thraupidae	*Trichothraupis melanops*	0	0	0	0.010	0.003	0.004	0.010	0.726	0.336	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus atrocapillus*	0.936	0.035	0.037	0.965	0.989	0.995	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus bartletti*	0.007	0.037	0.010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus cinereus*	0.006	0.004	0.059	0.001	0.132	0.972	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus obsoletus*	0.021	0.002	0.002	0.861	0.483	0.790	0.006	0.946	0.983	0.010	0.689	0.733	0.326	0.012	0.010	0.021	0.899	0.774	0	0	0
Tinamidae	*Crypturellus soui*	0.273	0.451	0.866	0.893	0.992	0.974	0.518	0.779	0.950	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus strigulosus*	0.081	0.013	0.004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus undulatus*	0.015	0.004	0.004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Crypturellus variegatus*	0.017	0.008	0.025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Nothocercus nigrocapillus*	0	0	0	0	0	0	0	0	0	0.706	0.006	0.003	0.043	0.256	0.187	0.049	0.484	0.524	0	0	0
Tinamidae	*Tinamus guttatus*	0.092	0.379	0.005	0.002	0.865	0.996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Tinamus major*	0.668	0.223	0.572	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	*Tinamus tao*	0.467	0.011	0.004	0.983	0.989	0.952	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trogonidae	*Pharomachrus antisianus*	0	0	0	0.993	0.517	0.022	0.803	0.988	0.513	0.936	0.969	0.934	0	0	0	0	0	0	0	0	0
Trogonidae	*Pharomachrus auriceps*	0	0	0	0	0	0	0.931	0.963	0.147	0.989	0.941	0.647	0.418	0.723	0.992	0.006	0.033	0.077	0	0	0
Trogonidae	*Pharomachrus pavoninus*	0.918	0.837	0.395	0.132	0.837	0.998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trogonidae	*Trogon collaris*	0.004	0.023	0.138	0.965	0.681	0.616	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trogonidae	*Trogon curucui*	0.058	0.024	0.003	0.181	0.593	0.983	0.004	0.198	0.379	0	0	0	0	0	0	0	0	0	0	0	0
Trogonidae	*Trogon melanurus*	0.007	0.157	0.052	0.004	0.820	0.984	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trogonidae	*Trogon personatus*	0	0	0	0	0	0	0.712	0.737	0.166	0.908	0.975	0.433	0.514	0.606	0.967	0.153	0.335	0.148	0.048	0.072	0.005
Trogonidae	*Trogon violaceus*	0.694	0.870	0.945	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trogonidae	*Trogon viridis*	0.243	0.024	0.106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdidae	*Catharus fuscater*	0	0	0	0	0	0	0.978	0.135	0.095	0.549	0.531	0.181	0.046	0.985	0.959	0	0	0	0	0	0
Turdidae	*Catharus ustulatus*	0.065	0.004	0.018	0.988	0.870	0.976	0.679	0.979	0.853	0.996	0.995	0.949	0.063	0.965	0.992	0.003	0.011	0.410	0.159	0.066	0.006
Turdidae	*Entomodestes leucotis*	0	0	0	0	0	0	0.473	0.473	0.645	0.444	0.478	0.463	0.009	0.066	0.105	0	0	0	0	0	0
Turdidae	*Myadestes ralloides*	0	0	0	0.990	0.272	0.004	0.940	0.978	0.922	0.961	0.771	0.928	0.788	0.996	0.972	0	0	0	0	0	0

Turdidae	*Turdus albicollis*	0.068	0.024	0.016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdidae	*Turdus amaurochalinus*	0.018	0.006	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdidae	*Turdus chiguanco*	0	0	0	0	0	0	0.001	0.003	0.002	0.001	0.001	0.004	0.003	0.001	0.002	0.001	0.017	0.008	0.001	0.001	0.001
Turdidae	*Turdus fuscater*	0	0	0	0	0	0	0	0	0	0	0	0	0.917	0.366	0.991	0.014	0.013	0.522	0.629	0.753	0.005
Turdidae	*Turdus hauxwelli*	0.037	0.041	0.038	0.125	0.932	0.603	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdidae	*Turdus ignobilis*	0.332	0.025	0.562	0.985	0.654	0.475	0.052	0.943	0.362	0	0	0	0	0	0	0	0	0	0	0	0
Turdidae	*Turdus leucops*	0	0	0	0.919	0.450	0.360	0.753	0.881	0.640	0.902	0.592	0.632	0.247	0.995	0.994	0	0	0	0	0	0
Turdidae	*Turdus nigriceps*	0.592	0.002	0.002	0.873	0.711	0.700	0.116	0.678	0.969	0	0	0	0	0	0	0	0	0	0	0	0
Turdidae	*Turdus serranus*	0	0	0	0	0	0	0.173	0.752	0.242	0.986	0.687	0.303	0.739	0.975	0.955	0.065	0.698	0.638	0	0	0
Tyrannidae	*Elaenia albiceps*	0.042	0.003	0.003	0.005	0.003	0.041	0.004	0.082	0.007	0.722	0.005	0.078	0.322	0.144	0.292	0.128	0.020	0.285	0	0	0
Tyrannidae	*Elaenia flavogaster*	0.010	0.096	0.483	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Elaenia gigas*	0.992	0.314	0.300	0.991	0.995	0.993	0.364	0.980	0.989	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Elaenia obscura*	0	0	0	0	0	0	0	0	0	0.298	0.194	0.067	0.254	0.347	0.351	0.567	0.916	0.934	0	0	0
Tyrannidae	*Elaenia pallatangae*	0	0	0	0	0	0	0.951	0.421	0.358	0.994	0.248	0.534	0.322	0.913	0.595	0.015	0.880	0.816	0	0	0
Tyrannidae	*Elaenia parvirostris*	0.290	0.028	0.025	0.371	0.839	0.884	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Elaenia spectabilis*	0.236	0.093	0.047	0.124	0.386	0.313	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Elaenia strepera*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Lophotriccus pileatus*	0	0	0	0.948	0.956	0.289	0.988	0.989	0.978	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Mionectes macconnelli*	0.003	0.013	0.013	0.499	0.984	0.992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Mionectes oleagineus*	0.335	0.192	0.770	0.958	0.995	0.994	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Mionectes olivaceus*	0.547	0.043	0.041	0.996	0.507	0.859	0.743	0.997	0.997	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Mionectes striaticollis*	0	0	0	0.325	0.724	0.520	0.263	0.847	0.337	0.994	0.562	0.919	0.894	0.175	0.993	0.139	0.310	0.325	0	0	0
Tyrannidae	*Tyrannus savana*	0.004	0.786	0.654	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Tyrannus tyrannus*	0.366	0.037	0.009	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannidae	*Zimmerius bolivianus*	0	0	0	0.956	0.209	0.005	0.737	0.926	0.972	0.385	0.912	0.733	0.009	0.082	0.092	0	0	0	0	0	0
Tyrannidae	*Zimmerius gracilipes*	0.036	0.030	0.087	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S4.3. Evaluation of the species distribution models (SDMs). SDMs were fitted for all 240 frugivorous bird species of the Manú Biosphere Reserve, Peru, based on mean annual temperature and precipitation. For each species, five SDM methods were fitted: generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (GBM), random forest (RF) and maximum entropy models (MAXENT). For all SDMs the evaluation metric for the evaluation dataset (20% of total number of occurrences) is given, in addition to the sensitivity and specificity values of the model. The best model per species was chosen by adding the sensitivity value to the specificity value of each model and selecting the model with the highest combined value. Evaluation values are provided for the TSS evaluation metric.

			TSS value of evaluation data					Sensitivity					Specificity					Best model selection
Family	Bird species	Number of GBIF occurrence records	RF	GBM	GAM	MAXENT	GLM	RF	GBM	GAM	MAXENT	GLM	RF	GBM	GAM	MAXENT	GLM	
Cardinalidae	*Cyanocompsa cyanoides*	864	0.759	0.701	0.537	0.555	0.533	0.845	0.851	0.881	0.833	0.845	0.913	0.844	0.654	0.720	0.687	RF
Cardinalidae	*Pheucticus aureoventris*	717	0.788	0.701	0.595	0.642	0.479	0.935	0.862	0.841	0.841	0.783	0.853	0.839	0.754	0.802	0.697	RF
Cardinalidae	*Pheucticus chrysogaster*	1375	0.833	0.687	0.485	0.568	0.426	0.938	0.814	0.887	0.938	0.858	0.895	0.873	0.598	0.629	0.567	RF
Cardinalidae	*Saltator aurantiirostris*	1244	0.866	0.695	0.611	0.653	0.639	0.971	0.916	0.925	0.849	0.921	0.896	0.779	0.690	0.804	0.717	RF
Cardinalidae	*Saltator coerulescens*	2571	0.711	0.609	0.474	0.467	0.488	0.847	0.913	0.785	0.928	0.819	0.864	0.698	0.693	0.539	0.668	RF
Cardinalidae	*Saltator grossus*	1042	0.853	0.782	0.684	0.709	0.672	0.925	0.940	0.861	0.876	0.831	0.928	0.841	0.823	0.833	0.840	RF
Cardinalidae	*Saltator maximus*	3332	0.785	0.648	0.528	0.571	0.527	0.901	0.827	0.827	0.869	0.813	0.884	0.821	0.701	0.699	0.716	RF
Columbidae	*Geotrygon montana*	803	0.762	0.712	0.610	0.620	0.648	0.936	0.924	0.898	0.898	0.904	0.826	0.789	0.710	0.722	0.743	RF
Columbidae	*Patagioenas cayennensis*	2881	0.748	0.588	0.548	0.544	0.499	0.869	0.846	0.825	0.875	0.933	0.878	0.741	0.723	0.673	0.565	RF
Columbidae	*Patagioenas fasciata*	2417	0.822	0.660	0.569	0.605	0.584	0.895	0.846	0.916	0.842	0.835	0.928	0.812	0.653	0.761	0.750	RF
Columbidae	*Patagioenas plumbea*	3003	0.806	0.680	0.600	0.552	0.580	0.863	0.871	0.769	0.853	0.851	0.943	0.809	0.831	0.700	0.727	RF
Columbidae	*Patagioenas subvinacea*	2334	0.793	0.656	0.595	0.592	0.573	0.864	0.817	0.779	0.794	0.736	0.929	0.839	0.816	0.797	0.837	RF
Corvidae	*Cyanocorax cyanomelas*	1213	0.842	0.759	0.632	0.686	0.578	0.932	0.899	0.886	0.916	0.945	0.909	0.860	0.745	0.770	0.633	RF
Corvidae	*Cyanocorax violaceus*	1689	0.902	0.855	0.764	0.826	0.792	0.973	0.967	0.937	0.919	0.928	0.929	0.888	0.828	0.907	0.864	RF
Corvidae	*Cyanocorax yncas*	1911	0.842	0.714	0.623	0.591	0.538	0.897	0.874	0.837	0.784	0.771	0.945	0.840	0.786	0.804	0.767	RF
Cotingidae	*Ampelioides tschudii*	263	0.962	0.867	0.796	0.696	0.633	0.981	0.962	0.923	0.808	0.923	0.981	0.906	0.873	0.888	0.710	RF
Cotingidae	*Ampelion rubrocristatus*	838	0.826	0.731	0.653	0.684	0.673	0.921	0.939	0.927	0.897	0.964	0.905	0.792	0.726	0.787	0.709	RF
Cotingidae	*Ampelion rufaxilla*	103	1	1	0.719	0.622	0.688	1	1	0.950	1	0.950	1	1	0.769	0.622	0.737	RF
Cotingidae	*Cephalopterus ornatus*	387	0.843	0.830	0.724	0.696	0.714	0.908	0.921	0.921	0.921	0.934	0.935	0.909	0.802	0.774	0.778	RF
Cotingidae	*Conioptilon mcilhennyi*	53	1	1	0.937	0.986	0.740	1	1	1	1	1	1	1	0	0.986	0.740	RF
Cotingidae	*Cotinga cayana*	536	0.878	0.887	0.821	0.847	0.802	0.953	0.953	0.915	0.943	0.962	0.925	0.935	0.906	0.904	0.840	GBM
Cotingidae	*Cotinga maynana*	398	0.950	0.925	0.842	0.808	0.857	0.975	0.987	0.937	0.987	0.975	0.975	0.938	0.906	0.817	0.883	RF
Cotingidae	*Gymnoderus foetidus*	812	0.907	0.851	0.794	0.784	0.786	0.975	0.950	0.981	0.969	0.963	0.932	0.901	0.813	0.813	0.824	RF
Cotingidae	*Iodopleura isabellae*	298	0.916	0.899	0.793	0.839	0.732	0.983	0.966	0.914	0.983	0.897	0.933	0.933	0.879	0.856	0.835	RF
Cotingidae	*Laniocera hypopyrra*	284	0.877	0.894	0.762	0.779	0.835	0.982	0.982	0.982	0.857	1	0.895	0.912	0.780	0.922	0.835	GBM
Cotingidae	*Lipaugus vociferans*	1839	0.831	0.804	0.749	0.777	0.748	0.959	0.967	0.972	0.942	0.964	0.872	0.837	0.777	0.835	0.784	RF
Cotingidae	*Oxyruncus cristatus*	141	0.929	0.857	0.678	0.678	0.591	0.964	0.964	0.786	0.857	0.786	0.964	0.893	0.892	0.818	0.805	RF
Cotingidae	*Pipreola arcuata*	457	0.879	0.835	0.688	0.719	0.677	0.967	0.901	0.890	0.912	0.879	0.912	0.934	0.798	0.807	0.797	RF
Cotingidae	*Pipreola frontalis*	51	1	1	0.862	0.656	0.864	1	1	1	0.900	1	1	1	0.862	0.756	0.863	RF
Cotingidae	*Pipreola intermedia*	94	0.947	0.842	0.731	0.669	0.537	0.947	0.947	1	0.947	0.895	1	0.895	0.731	0.722	0.641	RF
Cotingidae	*Porphyrolaema porphyrolaema*	72	1	1	0.936	0.956	0.861	1	1	1	1	0.929	1	1	0.936	0.956	0.933	RF
Cotingidae	*Querula purpurata*	1181	0.879	0.831	0.776	0.747	0.746	0.938	0.907	0.956	0.876	0.929	0.941	0.924	0.820	0.871	0.816	RF

Cotingidae	*Rupicola peruvianus*	1451	0.865	0.786	0.678	0.728	0.667	0.903	0.872	0.872	0.820	0.830	0.962	0.914	0.807	0.908	0.836	RF
Cotingidae	*Snowornis subalaris*	56	1	0.909	0.914	0.786	0.901	1	0.909	1	1	1	1	1	0.915	0.784	0.900	RF
Cotingidae	*Tityra cayana*	1097	0.787	0.675	0.593	0.568	0.558	0.819	0.953	0.902	0.935	0.930	0.968	0.721	0.691	0.629	0.625	RF
Cotingidae	*Tityra inquisitor*	613	0.739	0.688	0.524	0.571	0.498	0.812	0.940	0.897	0.821	0.974	0.927	0.748	0.627	0.749	0.524	RF
Cotingidae	*Tityra semifasciata*	1308	0.784	0.682	0.623	0.617	0.604	0.865	0.888	0.757	0.749	0.869	0.916	0.794	0.866	0.868	0.735	RF
Cracidae	*Aburria aburri*	410	0.915	0.841	0.711	0.735	0.707	0.963	0.915	0.878	0.817	0.805	0.951	0.927	0.832	0.918	0.901	RF
Cracidae	*Mitu tuberosum*	323	0.907	0.861	0.826	0.849	0.811	0.953	0.953	0.953	0.953	0.906	0.954	0.908	0.872	0.896	0.905	RF
Cracidae	*Ortalis guttata*	2049	0.828	0.708	0.617	0.594	0.603	0.918	0.903	0.807	0.861	0.847	0.910	0.810	0.809	0.734	0.756	RF
Cracidae	*Penelope jacquacu*	1067	0.863	0.807	0.743	0.725	0.727	0.910	0.943	0.953	0.948	0.934	0.953	0.864	0.791	0.776	0.794	RF
Cracidae	*Penelope montagnii*	829	0.825	0.789	0.649	0.666	0.604	0.922	0.922	0.880	0.904	0.892	0.904	0.867	0.770	0.761	0.712	RF
Cracidae	*Pipile cutoffmanensis*	817	0.857	0.808	0.794	0.783	0.688	0.894	0.875	0.919	0.919	0.944	0.963	0.933	0.875	0.864	0.744	RF
Icteridae	*Cacicus cela*	4304	0.810	0.681	0.648	0.645	0.648	0.906	0.903	0.874	0.938	0.893	0.904	0.778	0.773	0.707	0.755	RF
Icteridae	*Cacicus chrysonotus*	643	0.876	0.798	0.702	0.722	0.665	0.945	0.922	0.945	0.898	0.930	0.930	0.876	0.756	0.823	0.734	RF
Icteridae	*Cacicus haemorrhous*	964	0.785	0.701	0.557	0.575	0.579	0.873	0.825	0.915	0.905	0.952	0.912	0.876	0.641	0.670	0.627	RF
Icteridae	*Clypicterus oseryi*	300	1	0.967	0.899	0.919	0.856	1	0.967	0.983	0.950	0.950	1	1	0.916	0.969	0.906	RF
Icteridae	*Icterus icterus*	391	0.846	0.858	0.741	0.728	0.704	0.961	0.961	0.857	0.818	0.831	0.885	0.897	0.884	0.909	0.871	GBM
Icteridae	*Molothrus oryzivorus*	1674	0.735	0.638	0.546	0.574	0.505	0.905	0.844	0.878	0.884	0.862	0.824	0.794	0.667	0.689	0.642	RF
Icteridae	*Psarocolius angustifrons*	3654	0.876	0.758	0.674	0.679	0.655	0.924	0.856	0.851	0.818	0.841	0.952	0.900	0.822	0.862	0.814	RF
Icteridae	*Psarocolius atrovirens*	624	0.920	0.816	0.659	0.626	0.582	0.960	0.936	0.808	0.752	0.840	0.960	0.880	0.849	0.874	0.742	RF
Icteridae	*Psarocolius bifasciatus*	667	0.849	0.827	0.769	0.768	0.734	0.955	0.932	0.985	0.886	0.970	0.895	0.895	0.784	0.882	0.764	RF
Icteridae	*Psarocolius decumanus*	3404	0.737	0.566	0.466	0.483	0.472	0.850	0.804	0.918	0.734	0.961	0.887	0.762	0.547	0.743	0.510	RF
Odontophoridae	*Odontophorus balliviani*	57	0.909	0.909	0.646	0.731	0.552	1	1	1	1	0.909	0.909	0.909	0.646	0.726	0.643	RF
Odontophoridae	*Odontophorus speciosus*	206	0.878	0.780	0.681	0.613	0.671	0.976	0.878	0.854	0.878	0.854	0.902	0.902	0.828	0.734	0.816	RF
Odontophoridae	*Odontophorus stellatus*	236	1	0.957	0.879	0.780	0.797	1	1	1	0.915	1	1	0.957	0.879	0.865	0.797	RF
Picidae	*Celeus elegans*	536	0.878	0.886	0.773	0.810	0.755	0.971	0.914	0.924	0.952	0.933	0.907	0.972	0.850	0.858	0.822	GBM
Picidae	*Celeus flavus*	474	0.810	0.851	0.766	0.739	0.724	0.957	0.925	0.957	0.946	0.903	0.853	0.926	0.809	0.791	0.820	GBM
Picidae	*Celeus grammicus*	421	0.916	0.880	0.818	0.773	0.823	0.963	0.963	0.902	0.976	0.976	0.952	0.917	0.916	0.796	0.847	RF
Picidae	*Celeus spectabilis*	97	1	0.895	0.890	0.842	0.905	1	0.895	0.947	0.895	0.947	1	1	0.943	0.948	0.958	RF
Picidae	*Celeus torquatus*	256	0.863	0.882	0.743	0.776	0.722	0.961	0.961	0.922	0.980	0.941	0.902	0.922	0.822	0.796	0.781	GBM
Picidae	*Colaptes rubiginosus*	1759	0.808	0.716	0.527	0.638	0.538	0.933	0.846	0.710	0.867	0.855	0.875	0.869	0.817	0.771	0.680	RF
Pipridae	*Chiroxiphia boliviana*	340	0.926	0.824	0.653	0.665	0.679	0.956	0.926	0.794	0.838	0.971	0.971	0.897	0.859	0.827	0.708	RF
Pipridae	*Chiroxiphia pareola*	395	0.822	0.834	0.663	0.686	0.555	0.949	0.923	0.910	0.923	0.808	0.873	0.911	0.752	0.762	0.747	GBM
Pipridae	*Lepidothrix coeruleocapilla*	100	1	0.950	0.891	0.810	0.841	1	1	1	1	0.947	1	0.950	0.891	0.811	0.893	RF
Pipridae	*Lepidothrix coronata*	981	0.922	0.928	0.796	0.821	0.829	0.963	0.984	0.979	0.989	0.963	0.959	0.944	0.818	0.831	0.866	GBM
Pipridae	*Machaeropterus pyrocephalus*	362	0.931	0.917	0.784	0.770	0.814	0.958	0.972	0.889	0.889	0.944	0.972	0.944	0.895	0.881	0.869	RF
Pipridae	*Manacus manacus*	2059	0.851	0.711	0.628	0.590	0.596	0.919	0.866	0.924	0.934	0.874	0.932	0.845	0.704	0.656	0.722	RF
Pipridae	*Neopelma sulphureiventer*	50	1	1	0.821	0.681	0.658	1	1	1	0.800	1	1	1	0.821	0.881	0.658	RF
Pipridae	*Pipra chloromeros*	370	0.931	0.877	0.742	0.766	0.742	0.958	0.958	0.875	0.847	0.847	0.973	0.919	0.866	0.919	0.895	RF
Pipridae	*Pipra fasciicauda*	670	0.917	0.820	0.761	0.784	0.676	0.970	0.962	0.962	0.985	0.932	0.948	0.858	0.799	0.799	0.745	RF
Pipridae	*Xenopipo holochlora*	165	0.909	0.870	0.821	0.830	0.812	1	0.931	1	0.897	0.897	0.909	0.939	0.821	0.933	0.915	RF
Pipridae	*Xenopipo unicolor*	53	1	1	0.664	0.617	0.510	1	1	0.800	0.900	0.900	1	1	0.863	0.716	0.609	RF
Psittacidae	*Amazona farinosa*	1976	0.839	0.805	0.743	0.730	0.764	0.943	0.888	0.894	0.935	0.948	0.896	0.916	0.849	0.794	0.816	RF
Psittacidae	*Amazona mercenaria*	65	0.846	0.923	0.633	0.643	0.538	1	1	0.833	0.750	0.833	0.846	0.923	0.799	0.893	0.705	GBM
Psittacidae	*Amazona ochrocephala*	1458	0.841	0.749	0.711	0.720	0.743	0.917	0.948	0.913	0.941	0.920	0.921	0.801	0.798	0.779	0.823	RF

Psittacidae	*Ara ararauna*	1776	0.835	0.842	0.697	0.705	0.717	0.886	0.943	0.892	0.835	0.934	0.949	0.899	0.804	0.863	0.783	GBM
Psittacidae	*Ara chloropterus*	1304	0.823	0.765	0.696	0.720	0.698	0.892	0.896	0.973	0.938	0.923	0.931	0.870	0.723	0.781	0.775	RF
Psittacidae	*Ara macao*	1437	0.878	0.843	0.757	0.826	0.759	0.934	0.895	0.969	0.944	0.986	0.944	0.948	0.788	0.882	0.773	RF
Psittacidae	*Ara militaris*	219	0.837	0.840	0.609	0.543	0.544	0.837	0.953	0.977	0.674	0.907	1	0.886	0.631	0.868	0.637	GBM
Psittacidae	*Ara severus*	2178	0.870	0.753	0.686	0.666	0.651	0.927	0.946	0.862	0.937	0.836	0.943	0.807	0.824	0.730	0.815	RF
Psittacidae	*Aratinga leucophthalma*	2308	0.783	0.639	0.549	0.552	0.489	0.852	0.823	0.772	0.896	0.905	0.929	0.814	0.777	0.655	0.584	RF
Psittacidae	*Aratinga mitrata*	651	0.853	0.807	0.739	0.736	0.716	0.946	0.953	0.922	0.899	0.907	0.908	0.854	0.816	0.837	0.809	RF
Psittacidae	*Aratinga weddellii*	1240	0.890	0.853	0.770	0.795	0.770	0.967	0.929	0.967	0.975	0.996	0.923	0.923	0.803	0.819	0.774	RF
Psittacidae	*Bolborhynchus lineola*	276	0.909	0.927	0.749	0.837	0.756	0.982	0.982	0.891	0.982	0.964	0.927	0.945	0.858	0.855	0.792	GBM
Psittacidae	*Bolborhynchus orbygnesius*	100	0.900	0.900	0.757	0.750	0.564	1	0.900	1	1	0.850	0.900	1	0.758	0.750	0.714	RF
Psittacidae	*Brotogeris cyanoptera*	1903	0.918	0.881	0.768	0.774	0.773	0.981	0.952	0.957	0.968	0.899	0.937	0.929	0.811	0.806	0.874	RF
Psittacidae	*Brotogeris sanctithomae*	391	0.936	0.884	0.821	0.887	0.816	0.987	0.974	0.987	0.987	0.974	0.949	0.910	0.834	0.900	0.842	RF
Psittacidae	*Forpus modestus*	296	0.881	0.847	0.901	0.804	0.783	0.932	0.949	0.966	0.915	0.847	0.949	0.898	0.935	0.889	0.936	GAM
Psittacidae	*Nannopsittaca dachilleae*	46	1	1	0.979	0.973	0.734	1	1	1	1	0.889	1	1	0.979	0.973	0.846	RF
Psittacidae	*Orthopsittaca manilata*	1040	0.817	0.806	0.734	0.786	0.761	0.946	0.873	0.893	0.922	0.956	0.865	0.933	0.841	0.863	0.805	RF
Psittacidae	*Pionites leucogaster*	476	0.989	0.958	0.891	0.882	0.871	0.989	0.968	0.958	0.926	0.958	1	0.989	0.934	0.956	0.913	RF
Psittacidae	*Pionus menstruus*	3293	0.781	0.677	0.644	0.646	0.627	0.911	0.853	0.906	0.925	0.891	0.870	0.824	0.737	0.721	0.735	RF
Psittacidae	*Pionus tumultuosus*	544	0.862	0.798	0.661	0.699	0.678	0.963	0.954	0.944	0.870	0.889	0.899	0.844	0.717	0.828	0.790	RF
Psittacidae	*Primolius couloni*	239	0.958	0.917	0.876	0.877	0.835	0.958	0.938	0.979	0.958	0.896	1	0.979	0.897	0.919	0.940	RF
Psittacidae	*Pyrilia barrabandi*	432	0.907	0.930	0.910	0.887	0.849	0.965	0.965	1	0.977	0.965	0.942	0.965	0.911	0.911	0.884	GBM
Psittacidae	*Pyrrhura roseifrons*	117	0.957	1	0.899	0.772	0.809	1	1	1	0.957	1	0.957	1	0.899	0.815	0.810	GBM
Psittacidae	*Pyrrhura rupicola*	180	1	0.944	0.918	0.763	0.769	1	0.944	0.972	0.861	0.889	1	1	0.946	0.901	0.880	RF
Psittacidae	*Touit huetii*	140	1	1	0.808	0.875	0.851	1	1	0.964	0.964	1	1	1	0.843	0.911	0.851	RF
Psophiidae	*Psophia leucoptera*	184	1	0.919	0.807	0.827	0.863	1	1	0.946	0.919	0.973	1	0.919	0.862	0.909	0.890	RF
Ramphastidae	*Andigena hypoglauca*	365	0.917	0.765	0.611	0.713	0.582	0.958	0.861	0.944	0.903	0.778	0.959	0.904	0.666	0.809	0.804	RF
Ramphastidae	*Aulacorhynchus coeruleicinctis*	238	0.853	0.872	0.644	0.721	0.632	0.957	0.872	0.872	0.872	0.872	0.896	1	0.772	0.849	0.759	GBM
Ramphastidae	*Aulacorhynchus derbianus*	201	0.900	0.750	0.566	0.680	0.594	0.925	0.900	0.775	0.925	0.875	0.975	0.850	0.791	0.755	0.719	RF
Ramphastidae	*Aulacorhynchus prasinus*	1122	0.834	0.731	0.591	0.638	0.553	0.914	0.887	0.882	0.869	0.923	0.920	0.844	0.708	0.769	0.630	RF
Ramphastidae	*Capito auratus*	1622	0.922	0.839	0.770	0.781	0.749	0.959	0.978	0.874	0.893	0.877	0.963	0.861	0.896	0.888	0.872	RF
Ramphastidae	*Eubucco richardsoni*	660	0.931	0.909	0.820	0.797	0.827	0.947	0.954	0.962	0.901	0.939	0.985	0.955	0.858	0.896	0.888	RF
Ramphastidae	*Eubucco tucinkae*	86	1	1	0.924	0.936	0.937	1	1	0.941	0.941	1	1	1	0.983	0.995	0.937	RF
Ramphastidae	*Eubucco versicolor*	345	0.870	0.826	0.719	0.683	0.730	0.870	0.899	0.913	0.826	0.928	0.986	0.928	0.806	0.855	0.802	RF
Ramphastidae	*Pteroglossus azara*	499	0.930	0.859	0.739	0.820	0.763	0.980	0.909	0.838	0.970	0.919	0.950	0.950	0.901	0.850	0.844	RF
Ramphastidae	*Pteroglossus beauharnaesii*	265	0.925	0.943	0.824	0.837	0.805	0.981	0.943	0.962	0.943	1	0.943	1	0.862	0.894	0.805	GBM
Ramphastidae	*Pteroglossus castanotis*	1287	0.819	0.714	0.664	0.663	0.547	0.920	0.928	0.908	0.920	0.944	0.899	0.786	0.756	0.742	0.603	RF
Ramphastidae	*Pteroglossus inscriptus*	496	0.858	0.867	0.749	0.783	0.801	0.979	0.968	0.979	0.958	0.895	0.879	0.899	0.770	0.826	0.907	GBM
Ramphastidae	*Ramphastos tucanus*	2555	0.866	0.825	0.756	0.781	0.746	0.947	0.954	0.943	0.941	0.927	0.920	0.871	0.813	0.840	0.819	RF
Ramphastidae	*Ramphastos vitellinus*	1703	0.807	0.697	0.629	0.683	0.634	0.895	0.861	0.768	0.934	0.831	0.912	0.836	0.860	0.751	0.803	RF
Ramphastidae	*Selenidera reinwardtii*	598	0.908	0.891	0.761	0.776	0.742	0.966	0.983	0.958	0.924	0.856	0.942	0.908	0.803	0.852	0.886	RF
Steatornithidae	*Steatornis caripensis*	203	0.726	0.501	0.568	0.551	0.539	0.750	0.550	0.875	0.925	0.825	0.976	0.951	0.693	0.625	0.714	RF
Thraupidae	*Anisognathus igniventris*	1405	0.870	0.780	0.706	0.699	0.698	0.942	0.894	0.898	0.814	0.938	0.929	0.886	0.807	0.886	0.760	RF
Thraupidae	*Anisognathus somptuosus*	2194	0.897	0.793	0.748	0.717	0.676	0.949	0.877	0.896	0.863	0.866	0.948	0.913	0.851	0.854	0.809	RF
Thraupidae	*Buthraupis montana*	995	0.889	0.804	0.696	0.747	0.667	0.949	0.964	0.878	0.919	0.873	0.940	0.839	0.816	0.828	0.793	RF
Thraupidae	*Catamblyrhynchus diadema*	459	0.814	0.825	0.613	0.677	0.685	0.922	0.956	0.844	0.911	0.889	0.891	0.870	0.769	0.765	0.796	GBM

Thraupidae	*Chlorochrysa calliparaea*	491	0.918	0.898	0.752	0.760	0.772	0.929	0.939	0.969	0.898	1	0.990	0.959	0.783	0.862	0.772	RF
Thraupidae	*Chlorophanes spiza*	2100	0.800	0.706	0.599	0.579	0.564	0.908	0.842	0.949	0.915	0.866	0.893	0.864	0.650	0.663	0.698	RF
Thraupidae	*Chlorophonia cyanea*	976	0.791	0.686	0.665	0.653	0.653	0.889	0.974	0.894	0.788	0.841	0.903	0.713	0.771	0.864	0.812	RF
Thraupidae	*Chlorornis riefferii*	929	0.859	0.810	0.691	0.742	0.667	0.923	0.923	0.780	0.852	0.852	0.935	0.887	0.911	0.889	0.814	RF
Thraupidae	*Chlorospingus canigularis*	487	0.886	0.824	0.644	0.609	0.565	0.938	0.938	0.969	0.948	0.781	0.948	0.887	0.675	0.660	0.783	RF
Thraupidae	*Chlorospingus flavigularis*	1090	0.953	0.846	0.674	0.729	0.728	0.957	0.915	0.877	0.791	0.829	0.995	0.931	0.797	0.938	0.898	RF
Thraupidae	*Chlorospingus ophthalmicus*	1665	0.872	0.674	0.543	0.579	0.491	0.924	0.920	0.823	0.856	0.878	0.949	0.754	0.720	0.726	0.613	RF
Thraupidae	*Chlorospingus parvirostris*	193	0.897	0.897	0.727	0.685	0.598	0.923	0.949	0.949	0.897	0.821	0.974	0.949	0.778	0.787	0.776	RF
Thraupidae	*Cissopis leverianus*	1759	0.818	0.723	0.624	0.653	0.628	0.904	0.839	0.944	0.868	0.895	0.915	0.884	0.680	0.782	0.733	RF
Thraupidae	*Conirostrum cinereum*	1979	0.833	0.767	0.653	0.679	0.546	0.909	0.906	0.885	0.813	0.932	0.924	0.861	0.767	0.865	0.613	RF
Thraupidae	*Conirostrum speciosum*	553	0.804	0.771	0.604	0.581	0.493	0.876	0.924	0.848	0.981	0.924	0.928	0.847	0.755	0.598	0.569	RF
Thraupidae	*Cyanerpes caeruleus*	1633	0.798	0.676	0.589	0.624	0.531	0.866	0.888	0.913	0.875	0.791	0.933	0.789	0.675	0.748	0.740	RF
Thraupidae	*Cyanerpes cyaneus*	492	0.843	0.764	0.571	0.520	0.570	0.894	0.957	0.894	1	0.926	0.949	0.806	0.678	0.520	0.645	RF
Thraupidae	*Dacnis cayana*	2543	0.710	0.590	0.504	0.532	0.442	0.830	0.879	0.911	0.921	0.929	0.880	0.713	0.593	0.611	0.512	RF
Thraupidae	*Dacnis flaviventer*	556	0.901	0.892	0.772	0.801	0.828	0.973	0.973	0.937	0.946	0.955	0.928	0.919	0.835	0.855	0.872	RF
Thraupidae	*Dacnis lineata*	1418	0.802	0.772	0.601	0.598	0.629	0.851	0.902	0.888	0.870	0.775	0.951	0.866	0.713	0.727	0.853	RF
Thraupidae	*Delothraupis castaneoventris*	238	0.872	0.812	0.720	0.763	0.631	0.872	0.957	0.915	0.872	0.851	1	0.854	0.806	0.891	0.780	RF
Thraupidae	*Diglossa brunneiventris*	851	0.847	0.812	0.703	0.674	0.634	0.929	0.965	0.888	0.905	0.858	0.918	0.847	0.815	0.768	0.777	RF
Thraupidae	*Diglossa caerulescens*	633	0.874	0.787	0.624	0.643	0.634	0.984	0.960	0.848	0.808	0.896	0.890	0.827	0.775	0.835	0.736	RF
Thraupidae	*Diglossa cyanea*	2564	0.873	0.779	0.676	0.707	0.694	0.959	0.886	0.866	0.957	0.953	0.914	0.893	0.810	0.750	0.741	RF
Thraupidae	*Diglossa glauca*	282	0.928	0.910	0.848	0.827	0.813	0.982	0.982	0.927	0.927	0.964	0.946	0.929	0.920	0.900	0.849	RF
Thraupidae	*Diglossa mystacalis*	283	0.930	0.840	0.674	0.609	0.750	1	0.893	0.964	0.821	0.875	0.930	0.947	0.709	0.788	0.875	RF
Thraupidae	*Diglossa sittoides*	680	0.807	0.659	0.513	0.545	0.534	0.903	0.851	0.858	0.799	0.806	0.904	0.809	0.655	0.746	0.728	RF
Thraupidae	*Dubusia taeniata*	416	0.879	0.819	0.760	0.677	0.730	0.963	0.976	0.951	0.878	0.890	0.916	0.843	0.809	0.798	0.840	RF
Thraupidae	*Euphonia chlorotica*	994	0.716	0.711	0.486	0.518	0.463	0.912	0.892	0.938	0.928	0.778	0.804	0.819	0.548	0.589	0.683	RF
Thraupidae	*Euphonia chrysopasta*	774	0.844	0.850	0.763	0.765	0.768	0.902	0.902	0.948	0.922	0.967	0.942	0.948	0.814	0.844	0.801	GBM
Thraupidae	*Euphonia laniirostris*	2821	0.757	0.625	0.411	0.487	0.331	0.835	0.827	0.698	0.704	0.582	0.922	0.794	0.712	0.783	0.749	RF
Thraupidae	*Euphonia mesochrysa*	348	0.886	0.757	0.653	0.614	0.638	0.986	0.871	0.914	0.886	0.914	0.900	0.886	0.739	0.728	0.724	RF
Thraupidae	*Euphonia minuta*	349	0.784	0.770	0.676	0.738	0.622	0.870	0.928	0.928	0.870	0.841	0.914	0.843	0.747	0.868	0.782	RF
Thraupidae	*Euphonia rufiventris*	716	0.860	0.853	0.813	0.813	0.736	0.930	0.930	0.930	0.965	0.894	0.930	0.923	0.883	0.846	0.842	RF
Thraupidae	*Euphonia xanthogaster*	3722	0.855	0.717	0.597	0.646	0.602	0.898	0.826	0.737	0.799	0.946	0.957	0.890	0.862	0.847	0.656	RF
Thraupidae	*Iridophanes pulcherrimus*	198	0.925	0.925	0.753	0.793	0.790	1	1	0.923	0.974	1	0.925	0.925	0.829	0.817	0.789	RF
Thraupidae	*Iridosornis analis*	268	0.925	0.832	0.778	0.808	0.723	0.943	0.943	0.962	0.962	0.887	0.981	0.889	0.815	0.845	0.836	RF
Thraupidae	*Iridosornis jelskii*	150	0.933	0.900	0.639	0.690	0.668	0.933	0.900	0.867	0.933	0.833	1	1	0.773	0.756	0.834	RF
Thraupidae	*Lamprospiza melanoleuca*	151	0.900	0.933	0.880	0.773	0.834	1	0.933	1	1	1	0.900	1	0.880	0.774	0.834	GBM
Thraupidae	*Pipraeidea melanonota*	1333	0.802	0.687	0.568	0.570	0.593	0.869	0.781	0.773	0.885	0.777	0.933	0.906	0.795	0.685	0.816	RF
Thraupidae	*Piranga leucoptera*	537	0.859	0.726	0.653	0.695	0.686	0.933	0.819	0.876	0.876	0.943	0.925	0.907	0.777	0.819	0.744	RF
Thraupidae	*Piranga rubra*	1803	0.763	0.639	0.529	0.552	0.533	0.874	0.814	0.734	0.840	0.722	0.889	0.825	0.794	0.718	0.810	RF
Thraupidae	*Ramphocelus carbo*	5139	0.792	0.621	0.560	0.575	0.527	0.888	0.872	0.917	0.864	0.754	0.905	0.751	0.644	0.711	0.772	RF
Thraupidae	*Ramphocelus nigrogularis*	872	0.919	0.919	0.853	0.863	0.865	0.959	0.971	0.959	0.971	0.959	0.960	0.948	0.894	0.892	0.906	RF
Thraupidae	*Schistochlamys melanopis*	514	0.727	0.708	0.507	0.545	0.515	0.951	0.980	0.772	0.911	0.941	0.777	0.728	0.735	0.633	0.574	RF
Thraupidae	*Tachyphonus cristatus*	700	0.842	0.771	0.640	0.634	0.658	0.964	0.978	0.876	0.883	0.883	0.879	0.793	0.764	0.751	0.774	RF
Thraupidae	*Tachyphonus rufiventer*	201	0.875	0.850	0.692	0.630	0.609	0.950	0.975	0.900	0.925	0.975	0.925	0.875	0.791	0.705	0.634	RF
Thraupidae	*Tangara arthus*	2792	0.904	0.802	0.672	0.711	0.679	0.958	0.916	0.796	0.918	0.767	0.946	0.885	0.876	0.794	0.911	RF

Thraupidae	*Tangara callophrys*	356	0.929	0.958	0.882	0.832	0.842	0.986	1	1	0.929	0.900	0.944	0.958	0.881	0.903	0.942	GBM
Thraupidae	*Tangara chilensis*	2072	0.833	0.738	0.654	0.687	0.605	0.910	0.895	0.820	0.908	0.813	0.923	0.843	0.835	0.780	0.792	RF
Thraupidae	*Tangara chrysotis*	315	0.905	0.873	0.748	0.735	0.760	0.952	0.889	1	0.968	0.952	0.952	0.984	0.749	0.767	0.808	RF
Thraupidae	*Tangara cyanicollis*	2781	0.850	0.723	0.631	0.686	0.629	0.899	0.849	0.855	0.832	0.856	0.951	0.874	0.776	0.854	0.772	RF
Thraupidae	*Tangara cyanotis*	104	0.905	0.905	0.812	0.752	0.758	1	0.952	1	1	0.905	0.905	0.952	0.812	0.751	0.853	RF
Thraupidae	*Tangara gyrola*	3030	0.848	0.700	0.622	0.620	0.608	0.932	0.852	0.861	0.900	0.922	0.914	0.847	0.760	0.720	0.686	RF
Thraupidae	*Tangara mexicana*	1121	0.821	0.726	0.676	0.676	0.667	0.941	0.855	0.959	0.968	0.950	0.879	0.871	0.716	0.707	0.716	RF
Thraupidae	*Tangara nigrocincta*	477	0.884	0.800	0.696	0.731	0.587	0.916	0.947	0.853	0.916	0.905	0.968	0.853	0.843	0.816	0.681	RF
Thraupidae	*Tangara nigroviridis*	2226	0.887	0.751	0.733	0.784	0.690	0.948	0.900	0.859	0.895	0.893	0.939	0.852	0.874	0.889	0.798	RF
Thraupidae	*Tangara parzudakii*	1116	0.923	0.816	0.787	0.747	0.745	0.946	0.932	0.905	0.873	0.914	0.978	0.879	0.882	0.874	0.830	RF
Thraupidae	*Tangara punctata*	629	0.833	0.721	0.612	0.639	0.622	0.912	0.840	0.752	0.768	0.720	0.921	0.881	0.860	0.871	0.902	RF
Thraupidae	*Tangara ruficervix*	1112	0.896	0.864	0.749	0.782	0.727	0.927	0.918	0.886	0.891	0.864	0.968	0.946	0.863	0.889	0.863	RF
Thraupidae	*Tangara schrankii*	1400	0.900	0.835	0.727	0.719	0.677	0.953	0.957	0.896	0.892	0.928	0.946	0.879	0.832	0.827	0.749	RF
Thraupidae	*Tangara vassorii*	1355	0.852	0.748	0.675	0.662	0.658	0.915	0.907	0.926	0.941	0.926	0.934	0.841	0.749	0.721	0.732	RF
Thraupidae	*Tangara velia*	423	0.820	0.822	0.727	0.725	0.748	0.867	0.928	0.940	0.904	0.964	0.953	0.894	0.787	0.821	0.785	GBM
Thraupidae	*Tangara viridicollis*	436	0.919	0.896	0.823	0.807	0.776	0.977	0.965	0.942	0.930	0.895	0.943	0.931	0.880	0.877	0.878	RF
Thraupidae	*Tangara xanthocephala*	1354	0.877	0.787	0.731	0.724	0.698	0.932	0.902	0.860	0.849	0.860	0.945	0.886	0.870	0.874	0.838	RF
Thraupidae	*Tangara xanthogastra*	509	0.861	0.810	0.712	0.716	0.650	0.939	0.889	0.949	0.818	0.798	0.922	0.922	0.763	0.897	0.852	RF
Thraupidae	*Tersina viridis*	2109	0.780	0.701	0.593	0.635	0.601	0.866	0.943	0.881	0.873	0.908	0.915	0.758	0.713	0.762	0.693	RF
Thraupidae	*Thlypopsis sordida*	418	0.684	0.683	0.503	0.432	0.492	0.886	0.873	0.861	0.886	0.937	0.798	0.810	0.641	0.546	0.554	RF
Thraupidae	*Thraupis bonariensis*	1634	0.779	0.637	0.550	0.606	0.562	0.886	0.915	0.830	0.886	0.839	0.893	0.722	0.721	0.720	0.723	RF
Thraupidae	*Thraupis cyanocephala*	1810	0.846	0.727	0.625	0.671	0.598	0.893	0.851	0.916	0.876	0.955	0.953	0.876	0.709	0.795	0.643	RF
Thraupidae	*Thraupis episcopus*	9138	0.770	0.521	0.370	0.456	0.369	0.851	0.804	0.697	0.729	0.622	0.919	0.719	0.674	0.727	0.746	RF
Thraupidae	*Thraupis palmarum*	6090	0.744	0.585	0.484	0.506	0.464	0.858	0.881	0.830	0.935	0.813	0.887	0.703	0.653	0.572	0.649	RF
Thraupidae	*Trichothraupis melanops*	1032	0.907	0.805	0.754	0.775	0.739	0.961	0.941	0.922	0.887	0.877	0.947	0.864	0.831	0.888	0.862	RF
Tinamidae	*Crypturellus atrocapillus*	275	0.927	0.927	0.776	0.773	0.720	0.982	0.982	0.945	0.836	0.836	0.945	0.945	0.831	0.936	0.884	RF
Tinamidae	*Crypturellus bartletti*	282	0.964	0.946	0.878	0.875	0.868	1	0.964	1	0.929	0.964	0.964	0.982	0.878	0.947	0.904	RF
Tinamidae	*Crypturellus cinereus*	925	0.919	0.853	0.794	0.814	0.757	0.983	0.972	0.923	0.945	0.945	0.935	0.876	0.871	0.870	0.813	RF
Tinamidae	*Crypturellus obsoletus*	663	0.841	0.691	0.572	0.621	0.578	0.902	0.886	0.879	0.924	0.871	0.940	0.805	0.693	0.696	0.706	RF
Tinamidae	*Crypturellus soui*	1834	0.785	0.699	0.585	0.562	0.605	0.864	0.895	0.864	0.756	0.861	0.921	0.804	0.720	0.805	0.742	RF
Tinamidae	*Crypturellus strigulosus*	112	0.955	0.955	0.842	0.725	0.821	0.955	0.955	0.955	0.955	1	1	1	0.887	0.769	0.822	RF
Tinamidae	*Crypturellus undulatus*	1657	0.877	0.784	0.749	0.767	0.709	0.919	0.963	0.944	0.904	0.963	0.958	0.822	0.805	0.864	0.747	RF
Tinamidae	*Crypturellus variegatus*	447	0.888	0.876	0.782	0.763	0.732	0.955	0.944	0.955	0.876	0.933	0.933	0.933	0.827	0.887	0.800	RF
Tinamidae	*Nothocercus nigrocapillus*	122	0.917	0.833	0.762	0.748	0	0.917	0.917	1	1	0	1	0.917	0	0.748	0	RF
Tinamidae	*Tinamus guttatus*	300	0.933	0.867	0.825	0.880	0.836	0.967	0.917	0.933	0.983	0.983	0.967	0.950	0.891	0.896	0.853	RF
Tinamidae	*Tinamus major*	1034	0.857	0.809	0.768	0.772	0.748	0.910	0.896	0.975	0.871	0.876	0.947	0.913	0.793	0.901	0.872	RF
Tinamidae	*Tinamus tao*	255	0.882	0.882	0.664	0.651	0.644	0.980	0.960	0.940	0.840	0.880	0.902	0.922	0.724	0.809	0.764	RF
Trogonidae	*Pharomachrus antisianus*	564	0.874	0.836	0.756	0.775	0.763	0.927	0.862	0.881	0.927	0.936	0.947	0.973	0.876	0.847	0.826	RF
Trogonidae	*Pharomachrus auriceps*	1413	0.896	0.833	0.712	0.735	0.738	0.924	0.935	0.867	0.885	0.867	0.972	0.898	0.845	0.850	0.871	RF
Trogonidae	*Pharomachrus pavoninus*	222	0.955	0.841	0.797	0.736	0.738	0.955	0.864	0.909	0.841	0.909	1	0.977	0.888	0.895	0.829	RF
Trogonidae	*Trogon collaris*	1355	0.813	0.701	0.592	0.575	0.554	0.920	0.886	0.848	0.726	0.760	0.893	0.816	0.744	0.849	0.793	RF
Trogonidae	*Trogon cutoffrucui*	1157	0.817	0.757	0.647	0.586	0.539	0.904	0.930	0.912	0.820	0.939	0.913	0.827	0.734	0.766	0.600	RF
Trogonidae	*Trogon melanurus*	1422	0.833	0.780	0.730	0.744	0.717	0.910	0.918	0.910	0.914	0.953	0.923	0.863	0.819	0.830	0.764	RF
Trogonidae	*Trogon personatus*	1686	0.845	0.788	0.592	0.682	0.628	0.880	0.889	0.722	0.784	0.808	0.964	0.899	0.869	0.897	0.820	RF

Trogonidae	*Trogon violaceus*	222	0.818	0.886	0.693	0.648	0.718	1	0.932	0.864	0.864	0.977	0.818	0.955	0.828	0.785	0.740	GBM
Trogonidae	*Trogon viridis*	1592	0.787	0.734	0.636	0.631	0.666	0.884	0.926	0.871	0.852	0.868	0.903	0.808	0.765	0.778	0.798	RF
Turdidae	*Catharus fuscater*	380	0.894	0.825	0.678	0.600	0.619	0.973	0.865	0.838	0.797	0.784	0.921	0.961	0.839	0.802	0.835	RF
Turdidae	*Catharus ustulatus*	2058	0.829	0.673	0.589	0.571	0.583	0.922	0.804	0.738	0.743	0.740	0.908	0.869	0.851	0.828	0.842	RF
Turdidae	*Entomodestes leucotis*	334	0.896	0.806	0.705	0.708	0.651	0.910	0.896	0.925	0.925	0.955	0.985	0.910	0.780	0.782	0.695	RF
Turdidae	*Myadestes ralloides*	2199	0.902	0.762	0.672	0.685	0.651	0.938	0.887	0.848	0.841	0.823	0.964	0.875	0.827	0.842	0.827	RF
Turdidae	*Turdus albicollis*	1473	0.788	0.737	0.532	0.584	0.550	0.879	0.862	0.783	0.838	0.752	0.908	0.871	0.749	0.746	0.798	RF
Turdidae	*Turdus amaurochalinus*	1730	0.764	0.567	0.482	0.550	0.458	0.851	0.842	0.910	0.821	0.764	0.913	0.725	0.571	0.729	0.696	RF
Turdidae	*Turdus chiguanco*	2306	0.828	0.684	0.585	0.640	0.574	0.947	0.938	0.951	0.881	0.945	0.881	0.746	0.634	0.756	0.629	RF
Turdidae	*Turdus fuscater*	4362	0.823	0.712	0.594	0.624	0.636	0.899	0.914	0.895	0.829	0.940	0.924	0.798	0.699	0.795	0.696	RF
Turdidae	*Turdus hauxwelli*	577	0.913	0.878	0.822	0.828	0.746	0.965	0.922	0.922	0.930	0.870	0.948	0.957	0.900	0.898	0.877	RF
Turdidae	*Turdus ignobilis*	3427	0.821	0.681	0.642	0.625	0.623	0.913	0.888	0.839	0.771	0.805	0.908	0.793	0.803	0.854	0.817	RF
Turdidae	*Turdus leucops*	270	0.870	0.870	0.645	0.747	0.661	0.963	0.907	0.833	0.963	0.926	0.907	0.963	0.811	0.784	0.735	RF
Turdidae	*Turdus nigriceps*	270	0.867	0.790	0.657	0.542	0.597	0.941	0.882	0.922	0.980	0.882	0.926	0.907	0.736	0.561	0.715	RF
Turdidae	*Turdus serranus*	1312	0.839	0.748	0.656	0.686	0.637	0.935	0.935	0.808	0.866	0.862	0.905	0.813	0.846	0.820	0.775	RF
Tyrannidae	*Elaenia albiceps*	4855	0.808	0.655	0.550	0.634	0.543	0.892	0.867	0.916	0.869	0.829	0.916	0.789	0.635	0.766	0.714	RF
Tyrannidae	*Elaenia flavogaster*	2433	0.671	0.517	0.417	0.404	0.433	0.784	0.784	0.868	0.895	0.935	0.887	0.731	0.550	0.509	0.498	RF
Tyrannidae	*Elaenia gigas*	291	0.896	0.773	0.723	0.721	0.726	0.982	0.860	0.825	0.895	0.860	0.914	0.914	0.898	0.823	0.866	RF
Tyrannidae	*Elaenia obscura*	374	0.754	0.825	0.599	0.641	0.596	0.861	0.958	0.889	0.903	0.903	0.893	0.867	0.711	0.738	0.693	GBM
Tyrannidae	*Elaenia pallatangae*	772	0.838	0.740	0.576	0.670	0.623	0.870	0.890	0.883	0.857	0.929	0.968	0.851	0.693	0.812	0.693	RF
Tyrannidae	*Elaenia parvirostris*	643	0.675	0.550	0.468	0.460	0.426	0.815	0.790	0.782	0.895	0.887	0.860	0.760	0.685	0.563	0.539	RF
Tyrannidae	*Elaenia spectabilis*	242	0.792	0.729	0.577	0.567	0.589	0.833	0.875	0.896	0.875	0.958	0.958	0.854	0.680	0.692	0.631	RF
Tyrannidae	*Elaenia strepera*	53	0.818	0.667	0.756	0.546	0.476	1	0.667	0.889	0.667	1	0.818	1	0.868	0.879	0.472	RF
Tyrannidae	*Lophotriccus pileatus*	1337	0.904	0.796	0.639	0.712	0.621	0.949	0.949	0.840	0.938	0.907	0.951	0.846	0.798	0.775	0.714	RF
Tyrannidae	*Mionectes macconnelli*	306	0.884	0.767	0.721	0.651	0.643	0.900	0.817	0.883	0.817	0.867	0.984	0.951	0.838	0.833	0.776	RF
Tyrannidae	*Mionectes oleagineus*	1767	0.811	0.733	0.661	0.595	0.676	0.890	0.954	0.873	0.746	0.870	0.921	0.779	0.788	0.849	0.806	RF
Tyrannidae	*Mionectes olivaceus*	1252	0.871	0.752	0.655	0.660	0.549	0.951	0.848	0.951	0.827	0.646	0.920	0.904	0.704	0.831	0.902	RF
Tyrannidae	*Mionectes striaticollis*	1558	0.837	0.738	0.629	0.664	0.661	0.882	0.882	0.840	0.918	0.830	0.955	0.856	0.788	0.744	0.831	RF
Tyrannidae	*Tyrannus savana*	2292	0.633	0.503	0.320	0.377	0.319	0.751	0.771	0.817	0.848	0.943	0.882	0.729	0.504	0.528	0.375	RF
Tyrannidae	*Tyrannus tyrannus*	720	0.818	0.776	0.655	0.617	0.625	0.880	0.852	0.810	0.796	0.951	0.938	0.924	0.845	0.820	0.674	RF
Tyrannidae	*Zimmerius bolivianus*	197	0.949	0.897	0.694	0.649	0.683	0.974	1	1	0.897	0.846	0.974	0.897	0.694	0.752	0.837	RF
Tyrannidae	*Zimmerius gracilipes*	519	0.835	0.805	0.762	0.696	0.746	0.912	0.882	0.912	0.833	0.922	0.923	0.923	0.850	0.863	0.825	RF

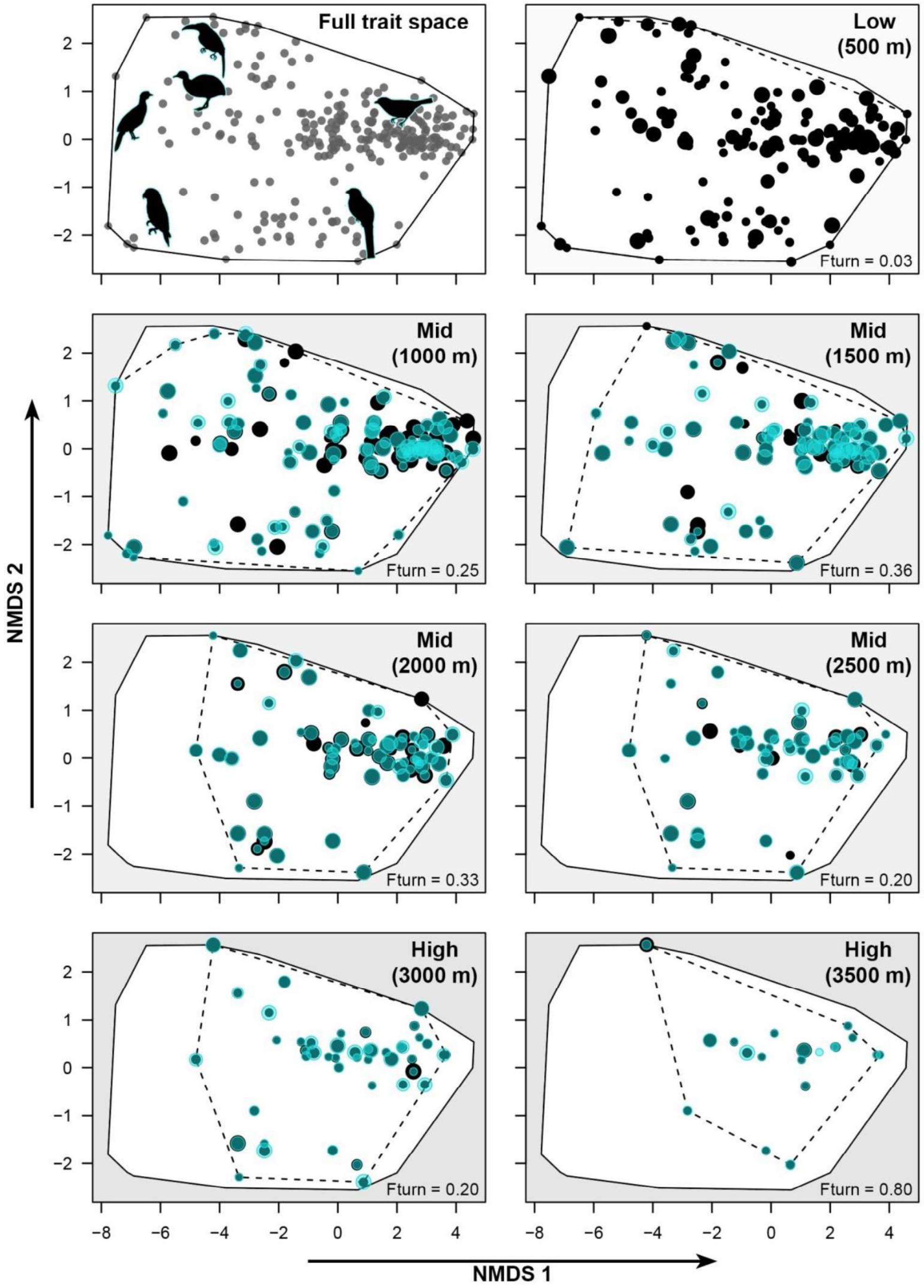

Figure S4.1. Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range contraction scenario*. The functional trait space is derived from Nonmetric Multidimensional Scaling (NMDS, based on Euclidean distances) which condenses the dissimilarity of ten morphological bird traits (bill width, bill length, bill height, tail length, tarsus length, tarsus sagittal width, tarsus lateral width, wing length, Kipp's distance and body mass) onto two axes

(NMDS 1, NMDS 2). Trait spaces are shown for the entire bird community (upper left) and for communities on each of the seven elevational levels (500 m to 3500 m, at 500 m steps). Black polygons illustrate the functional trait space of the entire bird community. Black stippled polygons illustrate the functional trait space of the current local community at the given elevation. Each dot represents one bird species (*n* = 240). Within each elevational level, dot size represents the probability of occurrence as derived from SDMs. Black dots represent current communities, transparent green dots represent occurrence probabilities under projected climate change (based on the RCP 6.0 scenario for 2070, MIROC5 climate model). Species-level changes are visible in four ways: (1) complete black dots indicate future loss of species, (2) complete green dots indicate future immigration of species, (3) dark green dots with a black ring indicate future decline in occurrence probability, and (4) dark green dots with a light green ring indicate future increase in occurrence probability. Functional turnover (Fturn) between current and projected future communities is provided in the bottom-right corner of each trait space (see Methods for details). Bird silhouettes in the upper left panel indicate the approximate location of key taxonomic groups in trait space (counterclockwise from top): toucans, tinamous, guans, parrots, trogons and tanagers.

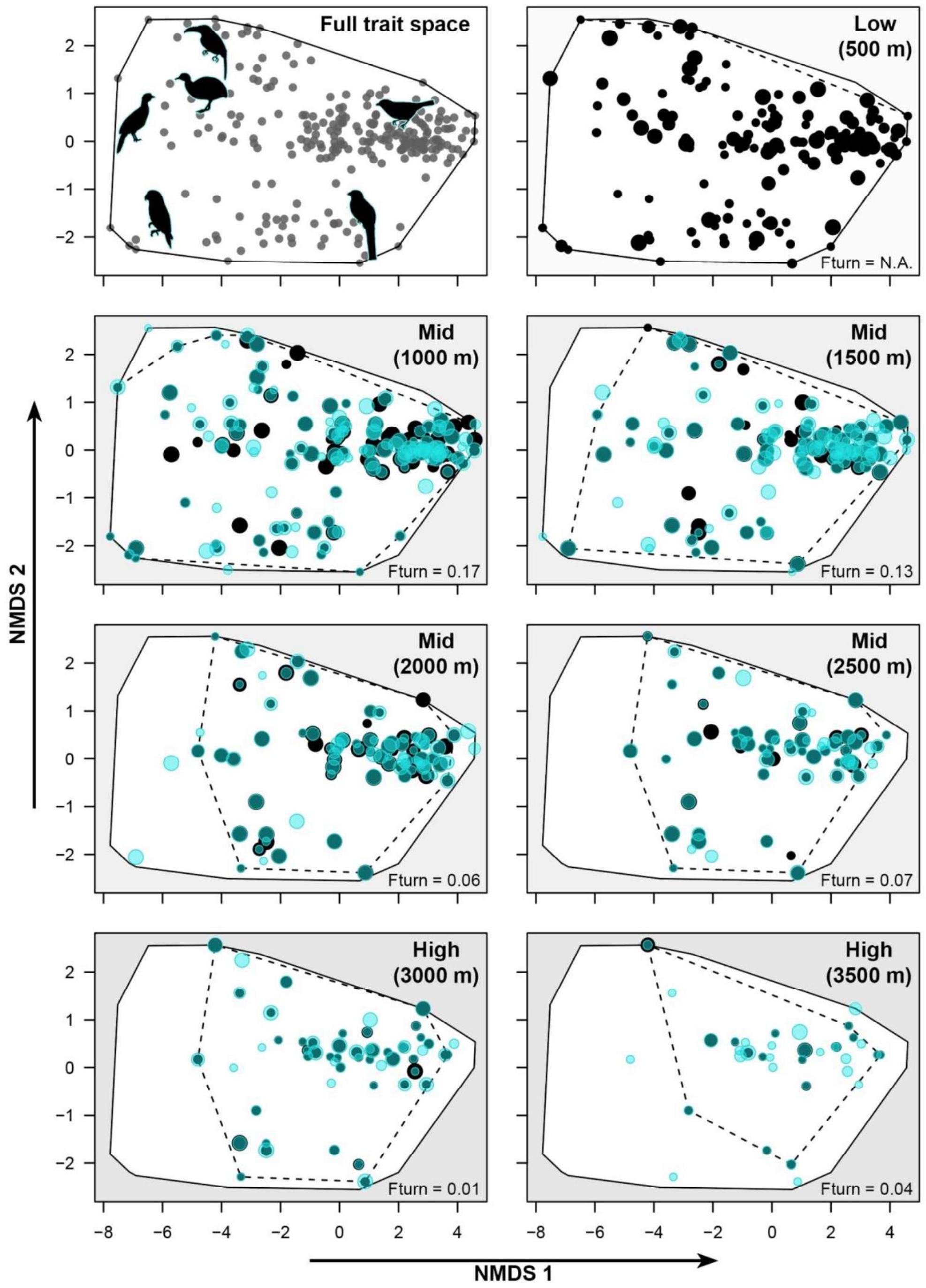

Figure S4.2. Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range shift scenario*. The functional trait space is derived from Nonmetric Multidimensional Scaling (NMDS, based on Euclidean distances) which condenses the dissimilarity of ten morphological bird traits (bill width, bill length, bill height, tail length, tarsus length, tarsus sagittal width, tarsus lateral width, wing length, Kipp’s distance and body mass) onto two axes (NMDS 1, NMDS 2). Trait spaces are shown for the entire bird community (upper left) and for communities on each of the seven elevational levels (500 m to 3500 m, at 500 m steps). Black polygons illustrate the functional trait space of the entire bird community. Black stippled polygons illustrate the functional trait space of the current local community at the given elevation. Each dot represents one bird species (n = 240). Within each elevational level, dot size represents the probability of occurrence as derived from SDMs. Black dots represent current communities, transparent green dots represent occurrence probabilities under projected climate change (based on the RCP 6.0 scenario for 2070, MIROC5 climate model). Species-level changes are visible in four ways: (1) complete black dots indicate future loss of species, (2) complete green dots indicate future immigration of species, (3) dark green dots with a black ring indicate future decline in occurrence probability, and (4) dark green dots with a light green ring indicate future increase in occurrence probability. Functional turnover (Fturn) between current and projected future communities is provided in the bottom-right corner of each trait space (see Methods for details). Bird silhouettes in the upper left panel indicate the approximate location of key taxonomic groups in trait space (counterclockwise from top): toucans, tinamous, guans, parrots, trogons and tanagers.

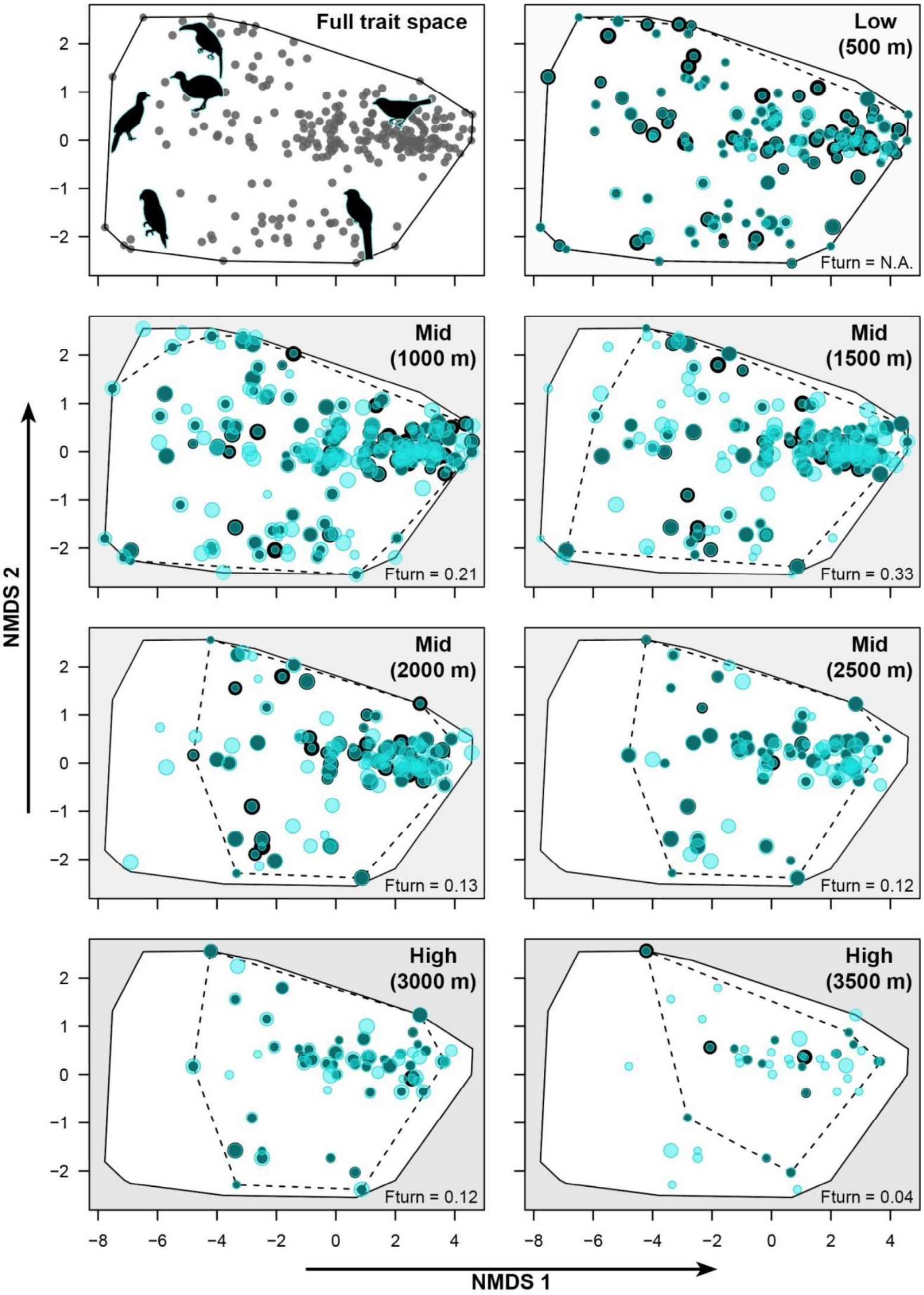

Figure S4.3. Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range expansion scenario*. The functional trait space is derived from Nonmetric Multidimensional Scaling (NMDS, based on Euclidean distances) which condenses the dissimilarity of ten morphological bird traits (bill width, bill length, bill height, tail length, tarsus length, tarsus sagittal width, tarsus lateral width, wing length, Kipp's distance and body mass) onto two axes

(NMDS 1, NMDS 2). Trait spaces are shown for the entire bird community (upper left) and for communities on each of the seven elevational levels (500 m to 3500 m, at 500 m steps). Black polygons illustrate the functional trait space of the entire bird community. Black stippled polygons illustrate the functional trait space of the current local community at the given elevation. Each dot represents one bird species (*n* = 240). Within each elevational level, dot size represents the probability of occurrence as derived from SDMs. Black dots represent current communities, transparent green dots represent occurrence probabilities under projected climate change (based on the RCP 8.5 scenario for 2070, MIROC5 climate model). Species-level changes are visible in four ways: (1) complete black dots indicate future loss of species, (2) complete green dots indicate future immigration of species, (3) dark green dots with a black ring indicate future decline in occurrence probability, and (4) dark green dots with a light green ring indicate future increase in occurrence probability. Functional turnover (Fturn) between current and projected future communities is provided in the bottom-right corner of each trait space (see Methods for details). Bird silhouettes in the upper left panel indicate the approximate location of key taxonomic groups in trait space (counterclockwise from top): toucans, tinamous, guans, parrots, trogons and tanagers.

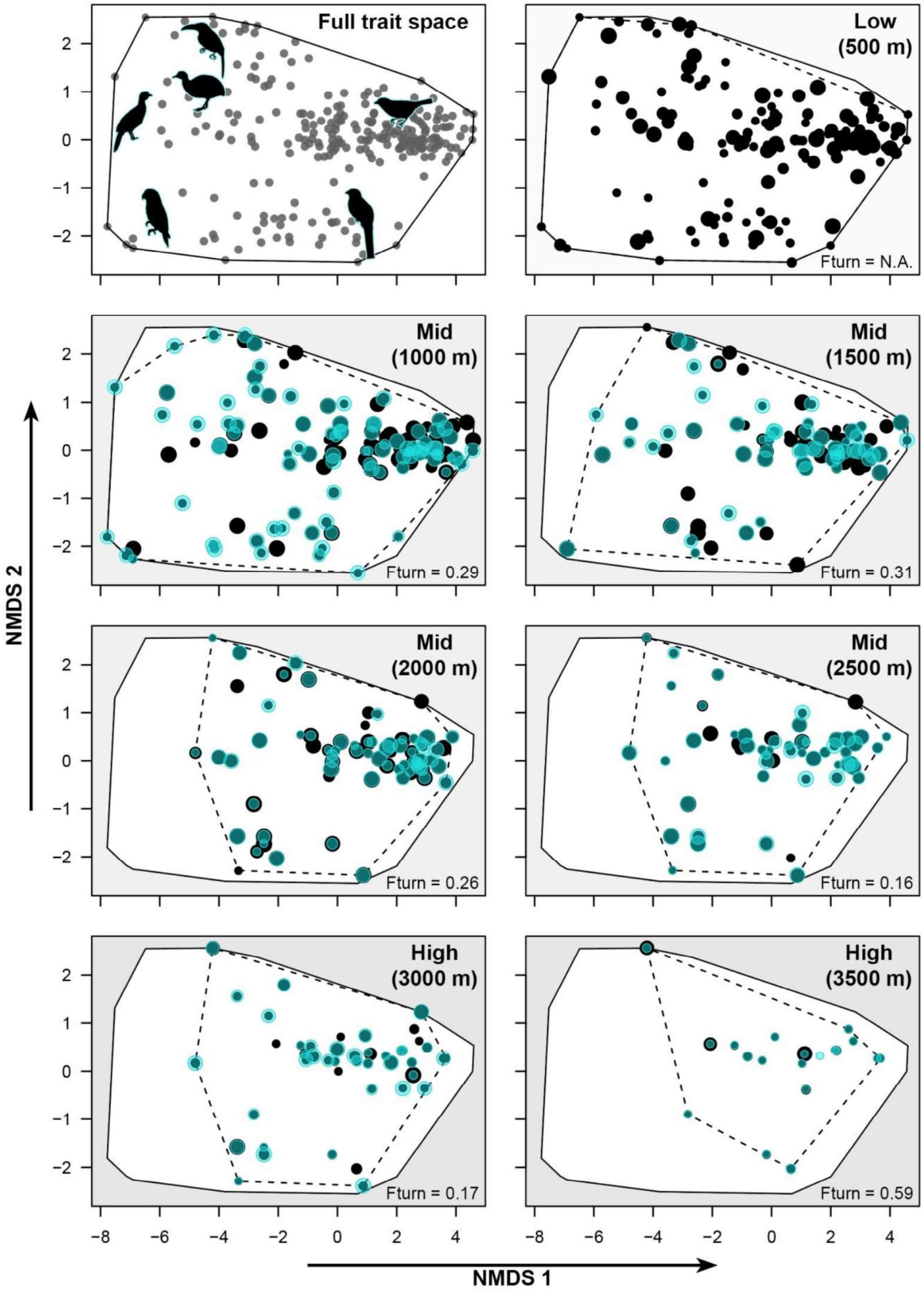

Figure S4.4. Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range contraction scenario*. The functional trait space is derived from Nonmetric Multidimensional Scaling (NMDS, based on Euclidean distances) which condenses the dissimilarity of ten morphological bird traits (bill width, bill length, bill height, tail length, tarsus length, tarsus sagittal width, tarsus lateral width, wing length, Kipp's distance and body mass) onto two axes

(NMDS 1, NMDS 2). Trait spaces are shown for the entire bird community (upper left) and for communities on each of the seven elevational levels (500 m to 3500 m, at 500 m steps). Black polygons illustrate the functional trait space of the entire bird community. Black stippled polygons illustrate the functional trait space of the current local community at the given elevation. Each dot represents one bird species (*n* = 240). Within each elevational level, dot size represents the probability of occurrence as derived from SDMs. Black dots represent current communities, transparent green dots represent occurrence probabilities under projected climate change (based on the RCP 8.5 scenario for 2070, MIROC5 climate model). Species-level changes are visible in four ways: (1) complete black dots indicate future loss of species, (2) complete green dots indicate future immigration of species, (3) dark green dots with a black ring indicate future decline in occurrence probability, and (4) dark green dots with a light green ring indicate future increase in occurrence probability. Functional turnover (Fturn) between current and projected future communities is provided in the bottom-right corner of each trait space (see Methods for details). Bird silhouettes in the upper left panel indicate the approximate location of key taxonomic groups in trait space (counterclockwise from top): toucans, tinamous, guans, parrots, trogons and tanagers.

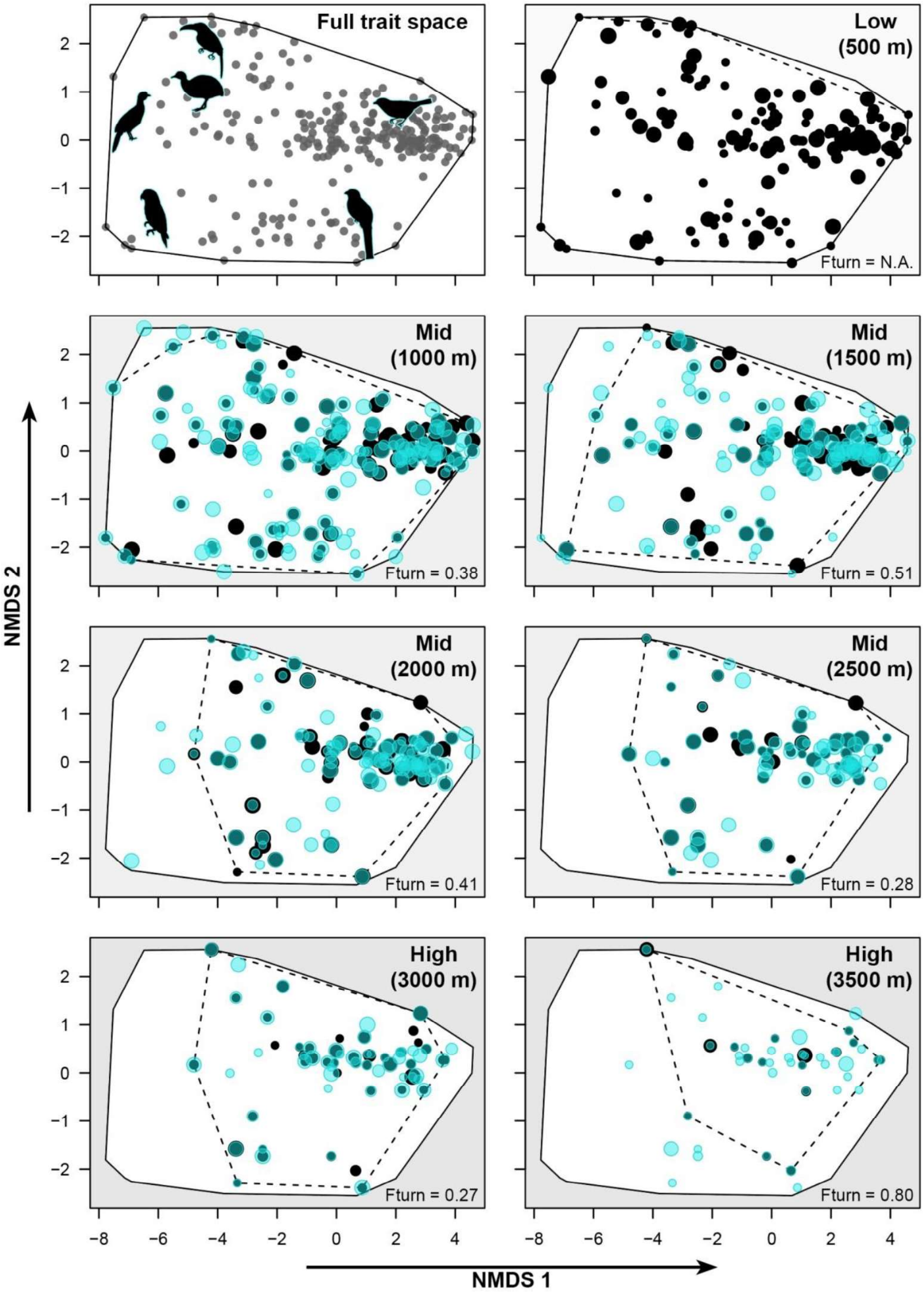

Figure S4.5. Projected changes in functional trait spaces of frugivorous birds under climate change assuming a *range shift scenario*. The functional trait space is derived from Nonmetric Multidimensional Scaling (NMDS, based on Euclidean distances) which condenses the dissimilarity of ten morphological bird traits (bill width, bill length, bill height, tail length, tarsus length, tarsus sagittal width, tarsus lateral width, wing length, Kipp's distance and body mass) onto two axes (NMDS 1, NMDS 2). Trait spaces are shown for the entire bird community (upper left) and for communities on each of the seven elevational levels (500 m to 3500 m, at 500 m steps). Black polygons illustrate the functional trait space of the entire bird community. Black stippled polygons illustrate the functional trait space of the current local community at the given elevation. Each dot represents one bird species (*n* = 240). Within each elevational level, dot size represents the probability of occurrence as derived from SDMs. Black dots represent current communities, transparent green dots represent occurrence probabilities under projected climate change (based on the RCP 8.5 scenario for 2070, MIROC5 climate model). Species-level changes are visible in four ways: (1) complete black dots indicate future loss of species, (2) complete green dots indicate future immigration of species, (3) dark green dots with a black ring indicate future decline in occurrence probability, and (4) dark green dots with a light green ring indicate future increase in occurrence probability. Functional turnover (Fturn) between current and projected future communities is provided in the bottom-right corner of each trait space (see Methods for details). Bird silhouettes in the upper left panel indicate the approximate location of key taxonomic groups in trait space (counterclockwise from top): toucans, tinamous, guans, parrots, trogons and tanagers.