UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
BIOLOGÍA EVOLUTIVA

Estructura genética, sociabilidad reproductiva y hábitat de la chara yucateca (*Cyanocorax yucatanicus*)

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS
PRESENTA:

FLAVIA TERMIGNONI GARCÍA

TUTORA DE TESIS: **DRA. PATRICIA ESCALANTE PLIEGO, INSTITUTO DE BIOLOGÍA, UNAM**

COMITÉ TUTOR: **DR. DANIEL PIÑERO DALMAU, INSTITUTO DE ECOLOGÍA, UNAM**

DRA. KATHERINE RENTON, INSTITUTO DE BIOLOGÍA, UNAM

MÉXICO, Cd. Mx. **ABRIL, 2017**

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P r e s e n t e

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 8 de febrero de 2016, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **TERMIGNONI GARCÍA FLAVIA** con número de cuenta **512012799** con la tesis titulada: **"Estructura genética, sociabilidad reproductiva y hábitat de la *chara yucateca*, (*Cyanocorax yucatanicus*)"**, realizada bajo la dirección de la **DRA. BERTHA PATRICIA ESCALANTE PLIEGO:**

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 7 de abril de 2017.

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DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

c.c.p. Expediente del (la) interesado (a).

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Dedicatoria

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Resumen

En *Cyanocorax yucatanicus* (la chara yucateca)*,* se ha reportado un sistema social reproductivo basado en la crianza cooperativa, una estrategia adaptativa evolutiva y altamente plástica, que abarca aspectos de la ecología, la conducta y la evolución. Además este córvido neotropical se distribuye en un gradiente ambiental en vegetación y clima en la Península de Yucatán y presenta variación geográfica en su morfometría, lo que lo respalda como modelo de estudio. La meta de esta tesis es comprender los patrones, procesos y mecanismos adaptativos en la chara yucateca ante el gradiente ambiental que habita, con un enfoque particular sobre el sistema social de esta ave. Esta tesis inicia con una revisión teórica y crítica de la evolución de la crianza cooperativa; continúa con un estudio sobre la ecología de la conducta en la chara yucateca, en aspectos de su sistema social (organización social) en relación al ambiente; y finaliza con análisis de asociación de los genotipos (a escala genómica) con el ambiente (temperatura y precipitación) y el fenotipo (morfometría). Los resultados de esta tesis sugieren que la chara yucateca ajusta su organización social y presenta adaptación local respecto al gradiente ambiental, inclusive en presencia de alto flujo génico. Las regiones candidatas a selección estan próximas a genes putativos codificantes de proteínas, para el desarrollo del sistema nervioso central (*CCDC85C),* secreción de hormonas asociadas a conducta (*SUCLA2* y *HTR2A)*, maduración osea (*IGF1*), para el funcionamiento de mecanismos sociales como la impronta y el aprendizaje (*ARC*), entre otros. En esta tesis se tomó ventaja de la complejidad del escenario

natural de las poblaciones de la chara yucateca, para acceder a los patrones, procesos y posibles mecanismos involucrados en la evolución y adaptación ante el gradiente ambiental que habita.

Palabras clave: Chara yucateca, crianza cooperativa, variación genética adaptativa, análisis de asociación, variación intraespecífica, sistemas sociales, organización social, gradiente ambiental.

Abstract

The Yucatan Jay (*Cyanocorax yucatanicus*) is a cooperative breeding bird in which subadult birds help their parents, expresing parental care to the younger birds (aloparental care). This reproductive system encompasses social aspects of ecology, behavior, and evolution, as it functions as a highly plastic and adaptive evolutionary strategy. This neotropical corvid is besides distributed in an environmental gradient along the Yucatan Peninsula that results morphometrical geographic variation, thus suggesting it could be a good model for studying the environment-phenotype-genotype interplay. The goal of this thesis was to understand the patterns, processes and adaptive mechanisms of the Yucatan jay to this environmental gradient and the origin of the cooperative breeding as an adaptive strategy to such a gradient. First, we made a theoretical review on the evolution of cooperative breeding. Then we analyzed the Yucatan jay's social organization in relation to the environment gradient, and finally we performed a series of association analysis between the genotype, the environment and the phenotype of specific individuals. We observed that there was a significant variation

in the social organization and the putative presence of local adaptations (at the molecular level) both related to the environmental gradient across the species range, and despite the presence of high gene flow. Footprints of natural selection were further observed near candidate coding genes associated to morphometric variation and environmental pressures. These genes are important for the development of the nervous system (*CCDC85C*, *SALL* y *KIAA0319)*, bones maturation (*IGF1*), behavioral hormone secretion (*SUCLA2* y *HTR2A*), imprinting and learning (*ARC*), etc. This thesis toke advantage of the Yucatan jay natural populations to disentangle the patters, processes and the possible mechanisms involved in their evolution and adaptation to the environment.

INTRODUCCIÓN

Las especies se pueden adaptar a condiciones ambientales particulares; dicho proceso ocurre mediante la diferenciación genética intraespecífica en las estrategias adaptativas (Maynard-Smith 1966; Rundle y Nosil 2005) y/o por la plasticidad fenotípica individual (West-Eberhard 2003; Whitman y Agrawal 2009; Volis et al., 2015). La diferenciación genética adaptativa, contrario a la plasticidad fenotípica, puede ser detectada en poblaciones que habitan ambientes heterogéneos dónde se promueven diferentes respuestas de selección (Zhivotovsky et al., 1996). Usualmente esta es causada por fuerzas de selección divergente (o selección disruptiva, Maynard-Smith 1966) y transmitida directamente (via pleiotropia) o indirectamente (via desequilibrio de ligamiento) en los genes causando el aislamiento reproductivo (Rundle y Nosil 2005). La plasticidad fenotípica, a pesar de que también juega un papel importante en la divergencia adaptativa y en el proceso de diversificación y especiación (Badyaev et al., 2002; Pfennig et al., 2010), resulta un reto para ser observada y comprobada en la naturaleza (se requiere un diseño experimental particular, transplantes recíprocos, cruzas controladas, etc. (Merila y Hendry 2014, Gianoli y Valladares 2012)). En cambio los complejos escenarios que ofrecen las poblaciones naturales distribuidas en ambientes heterogéneos a niveles espaciales y temporales, proveen modelos de estudio interesantes para comprender las respuestas a la selección y la ecología de la adaptación local (Zhivotovsky et al., 1996; Frichot et al., 2015).

Actualmente, la extensión de la síntesis evolutiva moderna (Extended Evolutionary

Synthesis, EES por sus siglas en inglés) que ha tenido apertura gracias al acelerado desarrollo tecnológico de la secuenciación genómica, ha permitido ampliar nuestra comprensión de los procesos evolutivos (Keller 2014; Laland et al., 2014; Laland et al., 2015). Para especies animales *no modelo*, los estudios de asociación del genotipo con el fenotipo y el ambiente ha permitido distinguir señales de adaptación local en poblaciones que viven en ambientes contrastantes (Kirk et al., 2011, Korte y Farlow 2013), incluso en presencia de altos niveles de flujo génico (Nielsen et al., 2009; Saint-Laurent et al., 2003; Mendez et al., 2010; Dennenmoser et al., 2014; Schweizer et al., 2016).

Los estudios de asociación aprovechan la complejidad de los escenarios que ofrecen las poblaciones naturales, como son los gradientes ambientales, para que a través de una búsqueda de señales de selección (a una escala genómica), se logre acceder a los procesos y mecanismos involucrados en la evolución y la adaptación (De Villemereuil et al., 2014; Frichot et al., 2013; Frichot et al., 2015). Por ejemplo, en *Philomachus pugnax* se han demostrado las posibles bases genéticas de conductas sociales como el "lekking" o "arenas", donde bloques de genes están encargados del desarrollo de diferentes fenotipos o morfotipos en las poblaciones, que son clave para el funcionamiento de la conducta reproductiva (Lamichhaney et al., 2016). Esta oportunidad de la biología evolutiva de encontrar señales de selección natural a nivel genómico a través de análisis de asociación ha permitido inferir el cambio genético, su naturaleza adaptativa y las causas ambientales o ecológicas (Günther y Coop 2013; Dennenmoser et al., 2014; Manthey y Moyle 2015; Schweizer et al., 2016).

Conocer los mecanismos biológicos del proceso adaptativo en poblaciones naturales es un campo de investigación en desarrollo, donde la genómica funcional se une con la genética de poblaciones (Schlötterer 2003). Desde el punto de vista del fenotipo y de las estrategias conductuales y sociales en vertebrados, las herramientas actuales posibiltan comprender mejor el papel y el potencial de la conducta en la evolución y en los cambios genéticos. Por ejemplo, es probable que estrategias sociales como la cooperación y el "altruismo", que durante décadas han sido un tema controversial dentro de la biología evolutiva y ecología (ver capítulo I), puedan ser abordadas desde una renovada perspectiva con los nuevos métodos genómicos y la extensión de la síntesis moderna (EES) .

Durante las últimas seis décadas en el mundo de la sociabilidad y sus diferentes formas (la cooperación, la eusocialidad, comunalidad, etc.) se ha buscado comprender el desarrollo y funcionamiento de dichas estrategias evolutivas, pues en muchos casos de estudio han resultado plásticas y adaptativas (Russell 2004, Pruett-Jones 2004, Burland et al., 2004, Woxvold y Mulder 2008, Geffen et al., 2011, Nichols et al., 2012, Schradin y Pillay 2005, Zöttl 2013). Algunos vertebrados ante nuevas presiones selectivas pueden cambiar de una reproducción independiente a un sistema social cooperativo (Koenig y Dickinson, 2004, Zöttl 2013), ajustando su conducta en respuesta a cambos ambientes, incluyendo el cambio climático (Charmantier et al., 2008). Conductas que pueden promover la cooperación, como el retraso en la reproducción y la dispersión de los individuos, impactan en el flujo génico (Beck et al., 2008; Berg et al., 2009), que a su vez es afectado por factores ecológicos y ambientales (Emlen 1995, Russell 2004, Koenig y Dickinson, 2004; Baglione et al., 2006;

Rubenstein y Lovette, 2007; Jetz y Rubenstein, 2011). Sin embargo, a pesar de que se han encontrado propiedades genéticas características de las poblaciones como estructura genética a una escala fina en poblaciones de vertebrados con crianza cooperativa (menos de 2 km) (McDonald et al., 1999, Woxvold et al., 2006, Delaney et al., 2008), incluyendo alta relación (similitud) genética entre individuos (Woxvold et al., 2006, Deheer y Vargo 2004, Geffen et al., 2011, Nichols et al., 2012) y niveles altos de endogamia (Haig et al., 1994, Johannesen y Lubin 1999,Beck et al., 2008), estas características no siempre y no solo se presentan en este tipo de sistemas sociales (Hatchwell 2010).

La chara yucateca (*Cyanocorax yucatanicus,* Dubois 1875)

La chara yucateca pertenece a la familia de aves Corvidae, aves modernas que diversificaron rápidamente a partir del Cretaceo-Terciario (K-T), hace unos 35 millones de años (Feduccia 1995; Feduccia 2003; Jarvis et al., 2014). Esta familia cosmopolita es reconocida por su gran éxito ecológico y sociabilidad (Blake y Vaurie 1962; Goodwin 1976; Madge y Burn 1994), siendo de las más ricas en conductas de crianza cooperativa en comparación con otras familias de aves (Edward y Naeem 1993, Arnold y Owens 1998; Ekman y Ericson 2006), ya que el 32% de los córvidos presenta cuidado aloparental en diferentes sistemas sociales reproductivos y el 69% de las especies viven en grupos familiares cohesivos (Ekman y Ericson 2006). Sin embargo, el sistema social o crianza cooperativa puede variar entre poblaciones de una misma especie (ejemplo: *Aphelocoma coerulescens* (Woolfenden y Fitzpatrick 1990). Algunos experimentos ecológicos han

demostrado que la sociabilidad en corvidos se desarrolla al existir cohesión de las unidades sociales lograda a través de la manipulación del *ambiente social* con el proceso de alimentación (Ekman y Ericson, 2006, Baglione et al., 2006, Canestrari et al., 2012). La crianza cooperativa es una estrategia altamente plástica (Saunders y Edwards, 2000; Koenig y Dickinson, 2004; Ekman y Ericson 2006), con múltiples transiciones donde una gran diversidad de fuerzas selectivas están involucradas (Ekman y Ericson, 2006) lo que hace difícil encontrar el estado ancestral (Ligon y Burt, 2004).

Los cuervos de América (conocidos tambien como "New World Jays"), están subdivididos en 7 géneros y 36 especies distribuidas desde el sur de Estados Unidos al sur de Argentina (Goodwin 1976, Madge y Burn 1994; Bonaccorso et al., 2010); son bien conocidos por una sociabilidad conspicua y conductas de crianza cooperativa (Brown 1987). Este grupo ha sido tomado con gran interés en estudios de evolución, ecología de la conducta cooperativa y sociobiología (Brown 1974, Peterson 1992). Al menos se conoce que la mitad de los cuervos de America tienen crianza cooperativa y que esta es una estrategia primitiva según se evaluó en estudios filogenéticos del grupo (Saunder y Edwards 2000).

Dentro de los cuervos de América, el género *Cyanocorax* ha resultado taxonómicamente complicado, dada la combinación tan diversa de coloración en el plumaje, tamaño y morfología (Bonaccorso et al., 2010). Sin embargo, el patrón más claro (usando varios métodos) es el del grupo monofilético *Cissilopha* (Hellmayr 1934; Blake y Vaurie 1962; Hardy 1969; Goodwin 1976; Monroe y Sibley 1993; Madge y Burn 1994; Bonaccorso y Peterson 2007; Bonaccorso et al., 2010). Formado por cuatro especies alopátricas: *C.*

yucatanicus, C. sanblasianus, C. beecheii y C. melanocyaneus, donde la especie hermana reconocidas es *C. dickeyi* (Bonaccorso et al., 2010).

Estas especies del grupo monofilético *Cissilopha* presentan algún grado de sociabilidad, exhibiendo variación en la muda como la coloración del plumaje, pico y anillo ocular, lo cual parece ser determinantes para la integración de los grupos sociales (Peterson 1991) y lograr la cohesión familiar (Ekman y Ericson, 2006). En las charas se ha visto que de esta manera se puede evitar hostilidades hacia los juveniles filopátricos (Hardy 1973, Raitt y Hardy, 1976; Peterson 1991). Principalmente en la chara yucateca, donde los fenotipos de edad y el repertorio vocal (~24 vocalizaciones distintas) son de los mas vistosos y variados del grupo, se ha observado que el grado de sociabilidad puede ser mayor que en las otras especies del grupo *Cissilopha* (Hardy 1961, 1973, 1974, 1979; Peterson 1991).

Por lo tanto, la chara yucateca resulta un modelo interesante de estudio por todas las características mencionadas arriba, pero sobre todo por distribuirse en un ambiente heterogéneo, el gradiente ambiental en clima y vegetación de la Península de Yucatán. Estudios previos ya han reportado variación morfométrica y dimorfismo sexual en relación a este gradiente ambiental (Chablé-Santos 1999).

La Península de Yucatán

Esta península es un área geográfica (N21˚30´, W92˚30´) cuyo clima (sistema Köppen) está determinado principalmente por un gradiente de precipitación, que a su vez

afecta al tipo de vegetación y se refleja en la diversidad florística y la cobertura vegetal. Esta península está sobre todo compuesta por planicies con alturas menores a 100m, aunque hacia el sur pueden alcanzar hasta de 250m con lomeríos de hasta 350m (Hubp y García-Arizaga 1999; Vázquez-Domínguez y Arita 2010). Por lo tanto, no existen barreras geográficas relevantes que limiten la dispersión de las poblaciones de aves, incluyendo la chara yucateca.

El gradiente climático divide de manera general a la península en dos áreas biogeográficas en sentido norte-sur (Duno-de Stefano et al., 2012). Originalmente es reconocida la unidad biogeográfica denominada Provincia Biótica Península de Yucatán (Miranda 1958; Barrera, 1962; Rzedowski, 1978; Estrada-Loera, 1991; Ibarra-Manríquez et al., 2002; Morrone, 2005; Vázquez-Domínguez y Arita, 2010) pero evaluando sus límites utilizando variables ambientales (clima y fisiografía) y grupos biológicos (plantas, aves, mamíferos, anfibios y reptiles (Lundell 1934; Goldman y Moore 1945; Barrera 1962; Lee 1980; Ibarra-Manríquez et al., 2002; Espadas-Manrique et al., 2003) se han llegado a reconocer hasta 14 subunidades (Ibarra-Manríquez et al., 2002; Morrone, 2005; Ramírez-Barahona et al., 2009). En el continuo de este gradiente climático se pueden notar tres tipos de vegetación predominantes (Rzedowski 1990): al norte se encuentra el bosque tropical caducifolio (BTC), al centro el bosque tropical subcaducifolio (BTSC) y hacia el sur el bosque tropical perennifolio (BTP) (Figuras 1 del capítulo II y III). La península se caracteriza también por una serie de fenómenos climáticos y meteorológicos, incluyendo los huracánes y el efecto de doble brisa marina originada por variaciones globales en la temperatura, como las

oscilaciones de El Niño (ENSO) (Gunn et al., 1995; Gunn et al., 2000).

Por lo tanto, esta tesis tiene como Objetivo General analizar la relación entre la variación genética y fenotípica de la chara yucateca con el gradiente ambiental (clima y vegetación) de la península de Yucatán. Como objetivos particulares están, el revisar la literatura en lo teórico y experimental de la evolución y ecología de la crianza cooperativa. El segundo objetivo es detectar la relación de aspectos del sistema social, como son la organización y composición social con el grandiente ambiental. El tercero, es buscar señales de selección natural mediante análisis de asociación genotipo-ambiente-fenotipo con un muestreo de la variación genética a nivel genómico. Estos objetivos se abordarán respectivamente en los tres capítulos de la tesis. La primera hipótesis plantea la existencia de relación entre aspectos del sistema social (como la organización social) con el gradiente ambiental de la península. La segunda plantea la asociación de la variación genética al gradiente ambiental y al fenotipo, como indicios de adaptación local.

CAPÍTULO I : Evolución de la crianza cooperativa

Muchos instintos son tan maravillosos, que su desarrollo parecerá probablemente al lector una dificultad suficiente para echar abajo toda mi teoría.

(Darwin 1859, Capítulo Vlll Origen de las especies)

Inicios en el estudio de la cooperación

En 1935 la revista Auk publicó por primera vez la presencia de una estrategia en aves que se conoce hoy como crianza cooperativa (*Cooperative Breeding*). En dicha publicación el naturalista A. Skutch reportó la observación de individuos extra-parentales asistiendo en la crianza, al llevar alimento a los polluelos o a la hembra en el nido. Previamente, Darwin (1859, Capítulo Vlll, pág. 303) ya había aceptado la complejidad en comprender a la luz de la selección natural la expresión de ciertas conductas que él mismo denominó de "altruistas", las cuales observó en insectos sociales donde los individuos estériles eran los principales actores. Tanto para Darwin como para A. Skutch, resultaba paradójica la presencia de la conducta "altruista", la crianza de la progenie por individuos que no son los padres genéticos ¿Cómo la selección natural puede favorecer a estos individuos?

Con el surgimiento de la síntesis entre la teoría de la evolución darwinista y la genética clásica mendeliana, Hamilton en 1964 teorizó sobre la conducta "altruista". Propuso que la

evolución de la conducta social "altruista" ocurre por la selección familiar, ya que el "verdadero altruismo" (se refería al sistema eusocial en algunos himenópteros) como lo llama él, no puede favorecerse por la selección natural. Lo que él hizo es justificar esta conducta en términos de un coeficiente de relación de parentesco genético, donde el altruista logra su adecuación mientras contribuye en la adecuación de un pariente porque comparten parentesco genético, a lo cual llamó de adecuación inclusiva. Así, aunque los ayudantes no se reproduzcan, sus alelos van a dispersarse a través de la reproducción de sus parientes y por eso es que ayudan. Aunque el modelo de Hamilton fue un giro de la visión altruista hacia la dispersión individual egoísta de los propios alelos (West-Eberhard, 1975), fue ampliamente aceptada.

Hasta este punto los naturalistas y los teóricos se unieron para comprender cuantitativamente esta forma de selección que actúa bajo los parámetros de las relaciones de parentesco entre los individuos, pero sobre todo para comprender la evolución de las sociedades basadas en actos de cooperación. Así nos lo demuestra Brown (1987) en su libro "*Helping and comunal breeding in birds*", donde propone poner en práctica, en el estudio de la crianza cooperativa en poblaciones naturales de aves, la regla de Hamilton mediante los elementos de la teoría de la adecuación inclusiva. Aunque surgieron una serie de limitantes con este modelo y, fueron los inicios del estudio cuantitativo en la crianza cooperativa, para ser más exactos eran los inicios de la sociobiología y de la ecología de la conducta.

En busca de los factores ecológicos de la cooperación

Durante más de siete décadas se han realizado arduas labores en varias ramas de la biología para entender los factores y mecanismos de la evolución de la sociabilidad que lleva a la cooperación o al "altruismo". En ecología se ha hecho especial hincapié en estudiar en detalle y a largo plazo poblaciones de varias especies de vertebrados con crianza cooperativa. Esto ha sido necesario ya que la cooperación no ha resultado tan fácil de predecir como la regla de Hamilton lo plasma. Esto ha permitido conocer el espectro de expresión de la crianza cooperativa. En aves por ejemplo, se ha visto que dentro de la crianza cooperativa se presentan varios sistemas de apareamiento (Woxvold y Mulder 2008), y se han categorizado en obligada o facultativa, con reproducción plural o singular, entre otras categorías (Brown 1987).

Los hallazgos dentro de la ecología de la conducta en vertebrados han sido importantes para comprender las causalidades ecológicas involucradas en sistemas sociales para que expresen estrategias de cooperación durante la crianza. Se han encontrado relaciones importantes entre la expresión de esta estrategia con la demografía (Canestrari et al., 2012), la calidad del territorio (Baglione et al., 2006), la variación climática (Rubenstein y Lovette 2007) y algunos factores fisiológicos, como las respuestas hormonales (Schoech et al., 1996, Rubenstein et al., 2008). Pero el patrón ecológico ante estos factores ha sido muy variado entre vertebrados e incluso entre paseriformes (Russell 2004, Pruett-Jones 2004). A pesar de esto, se destaca la importancia de la cooperación y de los individuos cooperantes en el éxito reproductivo de los grupos sociales (Cockburn 2008) y directamente en la

adecuación de los individuos reproductores (Reed y Walters 1996, Václav 2000, Williams y Hale 2008). Recientemente se ha detectado que la organización de los sistemas sociales (tamaño y composición) tiene un papel muy importante en la expresión de la crianza cooperativa (Schradin y Pillay 2005, Zöttl 2013).

Todos estos hallazgos nos permiten comprender los factores que influyen en una característica muy importante de la crianza cooperativa, el retraso en la dispersión de los juveniles de una unidad social (Emlen 1995, Rusell 2004). Esta característica es clave para la formación de un grupo social con diferentes grados de parentesco para que se forme la *viscosidad poblacional*, el escenario ideal para la evolución del "altruismo" según la regla de Hamilton. Sin embargo, para la ecología de la conducta, la pregunta aún sigue ¿Por qué hay poblaciones en estas condiciones de viscosidad poblacional donde no cooperan los individuos entre sí? Un sistema social con viscosidad poblacional no asegura que la cooperación será expresada, ya que éstas características resultan independientes en muchas especies (Ekman et al., 2004).

En busca del componente ancestral de la crianza cooperativa

En aves, en el orden Passeriforme, surge aparentemente un patrón en relación a la crianza cooperativa, pero en otros órdenes resulta como un componente ancestral que luego desaparece (Edwards y Naeem 1993). En el caso de los córvidos se ha mostrado un componente ancestral, que resulta altamente plástico y aunque gobernado en alguna

extensión por el componente filogenético, la presencia de la crianza cooperativa puede cambiar a escalas cortas en tiempo evolutivo (Berg et al., 2012 en el género *Aphelocoma).*

Diferentes estudios han analizado con ésta perspectiva el patrón ancestral en aves: Passeriformes, Edwards y Naeem 1993; Halicitidae y Apidae, Wcislo y Danforth 1997; aves comunales, Beauchamp 1999; Corvidae, Ekman y Ericson 2006; estúrnidos africanos con crianza cooperativa, Rubenstein y Lovette 2007; *Aphelocoma* por Berg et al., 2012. Estos estudios visualizan únicamente la divergencia de los linajes con alguna relación en las modalidades del sistema social. Las transiciones múltiples (Ekman y Ericson 2006) que pueden ser bidireccionales (Berg et al., 2011) o con patrones reversibles dentro de clados independientes (Wcislo y Danforth 1997), complican la inferencia de la modalidad social ancestral. Lo que ocurre con estudios de este tipo, basados en la comparación de la presencia actual (en tiempo ecológico) de una conducta social, es que no se conoce la historia demográfica de cada linaje para comprender las fuerza selectivas operantes que pudieron permitir las transiciones sociales dentro de los linajes y que pudieron llevar a estabilizar la crianza cooperativa.

Por esto, estudios intraespecíficos en este tema pueden resultar optimos para comprender la plasticidad de las estrategias sociales ante diferentes restricciones ecológicas (Baglione et al., 2006) y demográficas en el espacio y tiempo. Sobre todo permiten comprender aspectos que pueden ser fundamentales en el desarrollo de la historia de la crianza cooperativa, como son las fuerzas evolutivas implicadas, el flujo génico, la adaptación local y la deriva génica, que de otra forma no se pueden indagar (Helms y Cahan

2012).

Las fuerzas selectivas operantes y la viscosidad poblacional

La teoría Hamiltoniana fue un fundamento fuerte para la sociobiología y promovió el surgimiento de nuevas hipótesis. Con esta perspectiva D. S. Wilson (1975, 1977) incorporó una nueva dimensión en la genética de poblaciones: lo que él llamó el estudio de la estructura genética "*within the deme*". La estructura genética dentro de una población local no está dada sólo por los individuos, sino por el grupo donde se desarrollan las estrategias y por los grupos vecinos. En palabras de D. S. Wilson:

"Most organisms interact with a set of neighbors smaller than the deme (its trait group). Demes therefore are not only a population of individuals but also a population of groups (structured demes)"

Así surge la llamada “selección de grupo”, que no tuvo la misma aceptación que la selección familiar, aunque que en realidad la primera resulta solo una extensión de la segunda. Para el mismo D.S. Wilson resultaba intuitivo pensar que, cuando los grupos están compuestos enteramente por hermanos o parientes (*kin group*) el modelo es equivalente matemáticamente al modelo de selección familiar. Por esto y otras causas como la confusión semántica que maneja D.S. Wilson, para algunos autores (e.g. West et al., 2007) la selección de grupo tuvo una entrada más controversial y poco aceptada en la genética de poblaciones. Sin embargo, aunque fuera una extensión de la selección familiar, Wilson hace otras

observaciones que pueden resultar novedosas y con una aportación matemática.

Hay tres aspectos importantes del modelo de selección de grupo de D. S. Wilson (1975) que vale la pena recapitular. El primero es que dentro de la población local, los grupos embebidos varían en composición (viscosidad poblacional variable) y que como consecuencia de esa variación, el individuo presenta un promedio de “experiencias” y alelos que serán de su "tipo", los cuales estarán en mayor frecuencia que en toda la población local. Así, su conducta es dirigida diferencialmente hacia los de "su tipo". El segundo aspecto es que, si la evolución en la población local estructurada es diferente del modelo tradicional de selección individual, donde la varianza entre grupos es de cero, el umbral de esa varianza puede ser lo que permite la evolución del "altruismo". Desde este punto de vista se puede esperar que al menos una conducta "altruista débil" pueda ser un suceso común y recurrente, siempre y cuando exista ese umbral de varianza (Wilson 1975). Ante este estado de variación constante, si la población está sobreexplotando sus recursos y decrecen las tasas de alimentación, será seleccionada cualquier variación en la estrategia de grupo. Esta es una de las razones por las que J. Maynard Smith y Price (1973) consideran que la conducta cooperativa no es una estrategia evolutivamente estable. Sin embargo, el tercer aspecto contrapone éste argumento, y es que si se aumenta la adecuación de la unidad social o del grupo con la estrategia "altruista", puede evolucionar un estado de "inmunidad" contra los grupos que no son de ese "tipo" y por lo tanto se estabiliza el altruismo.

Actualmente se ha desarrollado la selección de grupo en lo que ahora se llama como la selección Multinivel (Wilson y Sober 1994). Este tipo de selección ha sido demostrada

experimentalmente en un estudio en poblaciones de codornices (Muir et al., 2013). A pesar de aún es controversial aunque no sea excluyente con la selección familiar, estes es uno de los aportes más importantes en el enmarañado mundo de la evolución de la conducta social "altruista".

El término más no el modelo de selección familiar es ampliamente usado en estudios a escala fina sobre la estructura genética en poblaciones naturales con crianza cooperativa. Estos estudios se hacen valer básicamente del coeficiente de relación (*r*) de Wright (1922) para poder discutir sobre el grado de parentesco genético dentro de los grupos y poblaciones, como lo propone Hamilton.

Para estimar el coeficiente de relación en poblaciones naturales entre los ensambles de individuos se usan generalmente marcadores genéticos polimórficos (como los microsatélites). Estos marcadores han permitido calcular la relación genética en varias especies animales, en las cuales se ha empleado el modelo de Hamilton para explicar la presencia de la sociabilidad y cooperación. Sin embargo, en algunas especies animales el modelo completo de Hamilton no parece ajustarce de manera tan simple como una relación genética. Esto ha sido en parte porque las especies eusociales (himenópteros), sobre las cuales Hamilton fundamentó su modelo, son organismos haploides-diploides, lo que provoca que las estimaciones de la media de relación genética dentro de las colonias sean altas en comparación con especies diploides. Por lo tanto, en especies eusociales el modelo de Hamilton resulta apropiado y apoya la teoría socio-biológica de la evolución del altruismo (Herrera 2012), pero entonces ¿Cómo se explicaría la evolución de la crianza cooperativa en

todo su espectro de expresión?

A pesar del inconveniente teórico y práctico del modelo de Hamilton (Gardner et al., 2011), los estudios sobre la estructura genética a escala fina en vertebrados con crianza cooperativa terminan con conclusiones paradójicas. Adjudican la posibilidad de que la selección familiar sea la fuerza evolutiva operante en alguno de los sexos (Hazlitt et al., 2004, Seddon et al., 2005, Andersson y Waldeck 2007). En algunos casos, cuando los valores de relación genética son bajos, se habla de una estructura genética familiar "incipiente" que puede explicar la cooperación dentro de las poblaciones (Hatchwell 2010). Lo que sucede es que la relación genética siempre está presente (ver algunos ejemplos de la Tabla 2). Por lo que ese camino nos lleva indudablemente a reconocer la importancia del parentesco en la evolución de la crianza cooperativa. Sin embargo, ha sido a través de estos estudios que se ha hecho evidente que en animales no-cooperativos también se encuentra una estructura familiar o de relación genética semejante a las cooperativas (Hatchwell 2010). Aparentemente, el retraso en la dispersión y la viscosidad poblacional tienden a crear esta estructura genética poblacional, donde la relación genética es más elevada y marcada dentro de las unidades más pequeñas, independientemente de la estrategia que sigan, cooperativa o no. Una visión más natural sobre la viscosidad poblacional incluye el tiempo como factor importante para comprender las relaciones de parentesco en toda su extensión. En palabras de J. Avise (2004):

"Interest kinship also arises for <u>any species</u> whose populations are <u>spatially structured</u>, perhaps along family lines. At increasingly greater depths in time, all conspecific individuals

are related to one another through an extended pedigree that constitutes the composite intraspecific genealogy of a species"

Con esta visión es difícil distinguir si cuando surgió el modelo de Hamilton, en realidad se estaba revelando una característica clave para la evolución de las sociedades cooperativas o por el contrario, se revelaba tan solo una propiedad natural de las poblaciones estructuradas en el espacio.

Tabla 2: Algúnos estudios a escala fina con marcadores polimórficos en poblaciones de diferentes especies con sociabilidad y crianza cooperativa para detectar relación genética.

Especie	**Sistema social y estrategia**	**Relación genética (r) Dentro del grupo**			**Autores**
		r	♀	♂	
Calocitta formosa	Crianza cooperativa	----------	0.13±0.04	0.02±0.01	Berg et al 2009
Manorina melanophrys	Colonia ¿cooperativos?	----------	0.07	0.42	Painter et al 2000
Perisoreus infaustus	Cooperativo facultativo?	----------	0.072	0.005	Li y Merilä 2010
Corcorax melanorhamphos	Cooperativo obligado	----------	-0.056±0.280	-0.042±0.289	Beck et al 2008
Struthidea cinerea	Crianza Cooperativa	0.3643 Entre grupos -0.0412 Macho/hembra adultos 0.0154	----------	----------	Woxvold et al 2006
Stegodyphus lineatus	Subsocial	0.22	0.28	0.34	Johannesen y Lubin 1999
Reticulitermes flavipes	Colonias	0.48	----------	----------	Deheer y Vargo 2004
Mungos mungo	Crianza cooperativa Comunal	Entre crias -0.105 Machos/hembras -0.42± 0.80	----------	----------	Nichols et al 2012

Crocuta crocuta	Clan matrilineal Cooperacion	----------	0.108±-0.050	0.07±-0.04	Watts et al 2011
Vulpes lagopus	Comunal	0.072± 0.222	----------	----------	Geffen et al 2011
Canis lupus	Clanes con cooperación	0.187- 0.500 Machos/hembras adultos 0.196-0.030	----------	----------	Geffen et al 2011

*Relación genética estimada con una matriz de medidas de las proporciones de alelos compartidas que son idénticas por descendencia entre individuos.

Genética de poblaciones: estudios de caso con crianza cooperativa

Los estudios con marcadores polimórficos en poblaciones naturales con crianza cooperativa se han desarrollado con diversas finalidades. En muchos de ellos (se pueden observar en los ejemplos de las tablas 2, 3 y 4) sus preguntas van enfocadas a la búsqueda de la paternidad y maternidad, para detectar el sistema de apareamiento (Berg 2005, Seddon et al., 2005, Townsend et al., 2009). Otros estudios se han hecho con la finalidad de encontrar la estrategia de dispersión (Painter et al., 2000), o los niveles de endogamia, para conocer el estado de las poblaciones y las medidas que deben tomarse para su conservación (Woxvold et al., 2006). Por ello y por los diferentes estadísticos o índices que emplean resulta complicado hacer una comparación. Sin embargo, la evaluación de las poblaciones a la luz de la genética de poblaciones tiende a revelar aspectos fundamentales para el entendimiento de los sistemas sociales, como la estructura genética de las poblaciones o de las unidades

sociales que se manejan en cada estudio (ver ejemplos de la tabla 2).

Por ejemplo, Nichols y colaboradores (2012) detectaron en poblaciones de una mangosta (*Mungos mungos*) variación temporal a lo largo de diez años en la relación genética dentro de los grupos sociales (alta relación dentro del grupo) y una estructura genética marcada que se mantuvo a lo largo de los diez años. Este tipo de estudios muestra un patrón a través del tiempo, y puede llevarnos a pensar que es una característica de un sistema social comunal con poliginia como el de la mangosta.

Por el contrario, las ratas desnudas (*Cryptomys damarensis*) expresan un interesante sistema eusocial con monogamia, donde el sesgo reproductivo por la pareja es de los más marcados en mamíferos. Incluso en la misma colonia, donde existe alta relación genética (r= 0.5), las parejas reproductivas que coexisten en la colonia no se reproducen mientras la pareja dominante lo esté haciendo (Burland et al., 2004). En este caso, se cree que el sesgo reproductivo puede ser una estrategia para evitar la endogamia (Burland et al., 2004). Semejante a este caso es en las hienas moteadas (*Crocuta crocuta*), donde es determinante el parentesco materno en la estructura de las redes sociales dentro de los clanes y en las afiliaciones entre hembras dentro del clan (Holekamp et al., 2012). Sin embargo, la relación genética entre hembras no es tan alta como en las ratas desnudas, aunque si es diferencial entre sexos. Este patrón es semejante en la urraca hermosa (*Calocitta formosa),* donde también las afiliaciones más fuertes son entre hembras mientras los machos se dispersan (Berg et al., 2009). Como contraste, en *Stegodyphus lineatus,* una araña "subsocial" sin crianza cooperativa, sus colonias tienen una alta relación genética (r= 0.22; Johannesen y

Lubin 1999).

Podemos notar en los ejemplos anteriores que las dimensiones y movilidad física de cada especie son un factor a considerar, sobre todo al analizar si la relación genética debe ser fundamental para la evolución de la sociabilidad cooperativa. En estudios como éstos que se pueden observar en los ejemplos de las tablas 2 y 4, hay particularidades que dificultan analizar la evolución de la crianza cooperativa bajo alguna condición o nivel particular de parentesco, sobre todo si cada uno se maneja en un contexto y dimensión particular.

Además, los análisis de paternidad, aunque revelan aspectos importantes del sistema social, únicamente lo hacen sobre el sistema de apareamiento, lo cual solo nos permite inferir si el acto de cooperación puede estar relacionado con una cooperación estricta o por el contrario por extra paternidad o múltiples parejas en un sistema comunal (Ejemplo 3). Estos trabajos nos sugieren que se requiere de mayor integración entre el trabajo empírico y teórico para la comprensión de la evolución de la crianza cooperativa (West et al., 2007).

Analizar cada estudio de caso puede ser muy revelador, ya que se pueden detectar al menos cuatro generalidades importantes. La primera es que efectivamente el retraso en la dispersión genera una asociación de parentescos entre los individuos, donde la viscosidad poblacional es variable en el tiempo y espacio. La segunda es que la dispersión de alguna vía es común, y ocurre naturalmente por hembras o machos (o por los dos). Lo cual es un mecanismo para evitar la depresión por endogamia. En este caso el sesgo reproductivo ocurre naturalmente por la misma viscosidad poblacional y demografía, y puede ser una

estrategia para evitar la reproducción entre congéneres. La tercera generalidad es que la migración representa una fuerza evolutiva importante dentro de estos sistemas, donde es común algún grado de extra paternidad y la dispersión diferencial entre sexos. Además, esto permite mantener el umbral de variación de la viscosidad poblacional. Y la cuarta generalidad es que el acto de cooperación en la crianza está dado principalmente por el sexo que no se dispersa, ya que es en este que reside la estructura poblacional y las relaciones de parentesco (Hatchwell 2010). Sobre este último punto todavía se requieren más estudios y comparaciones para considerarlo como una generalidad.

Una de las formas de evitar la consanguineidad en sociedades familiares con baja dispersión es el reconocimiento entre coespecíficos en los sistemas sociales (Mateo 2004, Moore 2007). Es bien sabido que las características de reconocimiento entre coespecíficos y parientes pueden ser perceptibles al ojo humano, pero en muchos casos no lo son (Leclaire et al., 2013). Estos mecanismos pueden dar estabilidad a la estrategia de cooperación en sociedades de animales (Komodeur y Hatchwell 1999, Sinervo et al., 2006), y van más allá de una simple relación genética (Höglund y Shorey 2003).

Dentro de los vertebrados con crianza cooperativa se ha visto que la relación parental resulta variable, pero la discriminación suele ser mayor donde se espera que los mecanismos de reconocimiento sean más sofisticados (Cornwallis et al., 2009). Este punto abre una perspectiva diferente sobre el retraso en la dispersión en ambientes con restricciones ecológicas y geográficas. El retraso en la dispersión, más que una característica clave para aumentar la viscosidad poblacional, puede también ser un mecanismo para que se desarrolle

la estructura de un sistema social. De esta manera conduce a interacciones sociales necesarias para que se reconozcan entre parientes y se evite la reproducción entre individuos altamente emparentados. Esto puede estar relacionado con el aprendizaje asociativo, que es un mecanismo de reconocimiento familiar (Komodeur y Hatchwell 1999).

El conocimiento que han dejado estos estudios nos permite comprender que para la evolución de la crianza cooperativa hay otros mecanismos a considerar y no solo la selección de grupo o la selección familiar. Hay otras fuerzas como la migración, que promueve variación en la viscosidad de una población, así como el tamaño del grupo también puede ser una condición para el mantenimiento de la cooperación en los grupos sociales (Schradin y Pillay 2005, Zöttl 2013).

Los estudios anteriores también nos muestran que un “mapa genético” de las relaciones parentales es una herramienta excelente para visualizar la microestructura genética y social en animales. Este también ayuda a identificar la vía de dispersión y niveles de migración, aunque es muy importante aplicarlo en paralelo con estudios de conducta y datos de historia de vida (Rollins et al., 2012).

Los estudios moleculares en grupos sociales nos dan el punto de inicio para analizar las fuerzas selectivas implicadas en la evolución social, al igual que para analizar los problemas evolutivos fundamentales relacionados con la asignación de los sexos, el sesgo reproductivo y por supuesto la naturaleza de la selección en poblaciones estructuradas jerárquicamente (Ross 2001). Estos estudios comparan la estructura genética de

poblaciones, asumiendo que todas las poblaciones emplean el mismo sistema social. Sin embargo es sabido que esto no siempre es así y que existe variación intraespecifica de los sistemas sociales en vertebrados (Lot 1991, Maher y Burger 2011, Zöttl 2013). Este aspecto es fundamental, pues esta variación puede estar asociada al tipo de condición ambiental y a un aislamiento reproductivo del tipo conductual entre poblaciones (Price 2008).

Distinguir si la divergencia entre linajes ocurre porque diferentes condiciones ambientales favorecen diferentes estrategias sociales o porque la estrategia social es la principal causa de divergencia, es casi imposible ya que resulta un reto desenmarañar ambos procesos (Price 2008). Pero detectar los procesos en la misma especie puede ser revelador, ya que la variación geográfica de estrategias permite investigar los procesos evolutivos (Burghardt y Schwarts 1999). Sin embargo, los estudios sobre la variación intraespecífica de los sistemas sociales ante diferentes condiciones ambientales son pocos (Baglione et al., 2006, Brashares y Arcese 2002; Schradin y Pillay 2005, Zöttl 2013) y parecen haber menos todavía los que incluyen el enfoque genético, mas allá de un análisis de paternidad o de estructura genética.

Tabla 3: Algúnos estudios a fina escala con marcadores polimórficos en poblaciones de diferentes especies con sociabilidad y crianza cooperativa para detectar la estructura genética

Especie	**Sistema social y estrategia**	**Fst/ Fis Promedio o rango**		**Autores**
		Fst	**Fis**	
Aves				
Manorina melanophrys	Colonia y grupos filopátricos ¿cooperativos?	Colonia 0.08±0.01 Grupo 0.04	0.02± 0.01	Painter et al 2000
Aphelocoma coerulescens	Crianza cooperativa	0.0735	0.082	Coulon et al 2008
Perisoreus infaustus	Cooperativo facultativo	0.043	0.032	Li y Merilä 2010
Corcorax melanorhamphos	Cooperativo obligado	0.124	----------	Beck et al 2008
Struthidea cinerea	Crianza cooperativa	0.1901	----------	Woxvold et al 2006
Sitta pusilla	Crianza cooperativa	0.01±0.02	----------	Haas et al 2010
Picoides borealis	Crianza cooperativa	0.19	----------	Haig et al 1994
Manacus manacus	" Lek" de machos	0.001 entre leks	0.02 dentro leks	Höglund y Shorey 2003
Invertebrados				
Stegodyphus lineatus	subsocial	0.14	-0.113±0.070	Johannesen y Lubin 1999

Reticulitermes flavipes	Colonias/eusocial	0.29	-0.24	Deheer y Vargo 2004
Mamíferos y peces				
Mungos mungo	Crianza cooperativa/ Comunal	0.129	-0.090	Nichols et al 2012
Neolamprologus pulcher	Crianza cooperativo	0.040	0.020	Stiver et al 2004
Aluatta seniculos	Crianza cooperativa	0.225	----------	Pope 1992
Crocuta crocuta	Clan matrilineal Cooperación	0.108	0.055	Holekamp et al 2012
Ctenodactylus gundi	Cooperativo	0.10	–0.17 / –0.09	Nutt 2008

Tabla 4: Algúnos estudios con análisis de paternidad en poblaciones de diferentes especies con sociabilidad y crianza cooperativa para detectar el sistema de apareamiento.

Especie	**Estrategia social conocida***	**Después del análisis genético**	**Sistema apareamiento con pruebas genéticas**	**Autores**
Corvus brachyrhynchos	Crianza cooperative (una pareja)	algún grado de extra paternidad	Hembra reproductiva monopoliza maternidad. Paternidad 82.7% Ayudantes 6.9% Flotantes 10.4%	Townsend et al 2009
Acrocephalus sechellensis	Crianza cooperativa	Aspecto comunal	Extra paternidad 25–53% Extra maternidad 6% Hembra dominante 77–98% Macho dominante 46–	Richardson et al 2001

			75% Hembras ayudantes 7–28% Machos ayudantes 11%	
Monias benschi	Crianza cooperativa	Grupos con monogamia y grupos con polyginandria	Ambos padres del grupo filopátrico 68%	Seddon et al 2005
Meles meles	Sociales facultativos Competencia por reproducción entre hembras. Sin crianza cooperativa	Aspecto comunal	Maternidad 44% Paternidad 15%	Carpenter et al 2005
Calocitta formosa	Crianza Cooperativa Observación indican una pareja reproductiva	Genético demuestra extra paternidad y maternidad	Pareja= hembra 74.1% y macho 58.8%. Hembras ayudantes 8.8% Machos flotantes 14.7%	Berg 2005
Cryptomys damarensis	Eusocial	Colonias con alto sesgo reproductivo	Hembra reproductiva monopolize maternidad Paternidad 80%	Burland et al 2004

*Estrategia social conocida en la bibliografía o por observaciones de los autores.

La aportación de los modelos experimentales

La experimentación con especies modelo y principalmente con microorganismos ha permitido integrar los aspectos teóricos de la evolución de la sociabilidad cooperativa ante ambientes heterogéneos con un enfoque de genética de poblaciones. Recientemente con microbios se ha visto que la cooperación social es una estrategia que expresan varias especies (Crespi 2001). Por ejemplo se ha descubierto que las bacterias son organismos altamente sociales que se comunican vía señales moleculares, se mueven colectivamente sobre superficies y hacen comunidades en forma de *biofilms* (Griffin et al., 2004).

Con *Pseudomonas aeruginosa*, donde la estrategia de cooperación es representada por la producción de sideróforos (relacionados con la virulencia en el hospedero), la cooperación aumenta con el nivel de relación genética o parental de las colonias, lo cual apoya la selección familiar (Griffin et al., 2004); aunque, ante una dispersión altamente limitada se puede generar competencia entre parientes. Por el contrario, la cooperación se favorece si es del tipo "budín" (moderada), formándose pequeños grupos con alto nivel de relación genética que reducen la competencia local entre parientes (Kümmerli et al., 2008).

En el mismo contexto y bajo diversas condiciones ambientales, los individuos desertores (no cooperantes) evolucionan en ambientes uniformes y la cooperación se favorece cuando las metapoblaciones se encuentran en un ambiente con parches heterogéneos (Dumas y Kümmerli 2012). De esta manera los competidores son menos propensos a invadir ambientes heterogéneos donde domina la cooperación. Otro aspecto

interesante con *P. aeruginosa* es que la represión de la competencia (RC por sus siglas en inglés) *per se*, opuesto al incremento de las relaciones parentales, es lo que promueve un aumento en la cooperación (Kümmerli et al., 2010), ya que la cooperación se favorece cuando se alinean los intereses de los individuos con los intereses del grupo social (Frank 2003)

Por otro lado, en *Pseudomona flourescens*, los *biofilms* más diversos son menos susceptibles a la invasión de competidores o desertores a la cooperación, ya que en primer lugar hay menos recursos disponibles para un invasor y los grupos diversos son más productivos que los grupos clonales (Brockhurst et al., 2006). De esta manera, se demuestra que la diversificación en diferentes nichos ecológicos favorece la cooperación y dismunuye la competencia local de recursos entre individuos. Esto demuestra que la expresión de la sociabilidad y la cooperación no tiene una relación obligada con algún clima o hábitat en particular. Aunque el hecho de generar en el ambiente condiciones nuevas puede estimular la selección de estrategias sociales nuevas para interactuar con una situación *de novo*. Por ejemplo, en *Drosophila ananassae,* cuando se le somete a nuevos ambientes estresantes (de temperatura) aumenta la variación fenotípica, se promueve la conservación de una alta variación genética y la variación en estrategias de apareamiento son más pronunciadas (Sisodia y Singh 2009).

Otro experimento de gran aportación en el tema, es el desarrollado por Foster y colaboradores (2004) con *Dictyostelium discoideum*. Ellos encontraron que la pleiotropía es un mecanismo que puede estabilizar la cooperación. El gen responsable *dimA* tiene dos

efectos contrastantes, es requerido para recibir la señal de una molécula que causa la diferenciación entre las células que fungirán como tallos, y las que morirán a favor de la reproducción. Este estudio demuestra que la evolución de conexiones pleiotrópicas entre desertores y el costo personal pueden estabilizar las adaptaciones cooperativas. La pleiotropia puede ser entonces la regla en lugar de la excepción para muchas estrategias conductuales y sociales, ya que es el producto de procesos motores sensoriales, emotivos e integrativos (Keller 2009). De esta manera, la pleiotropía provee una vía para limitar la inestabilidad de las sociedades en el desarrollo de una estrategia, lo que puede permitir la evolución de la cooperación.

Todos estos hallazgos no dejan de ser modelos experimentales bajo condiciones controladas y poco representativas respecto a las poblaciones naturales de vertebrados. Pero no podemos negar los resultados sustanciales que se han obtenido y que permite replantearnos la evolución de la crianza cooperativa. Aunado a los hallazgos de estos estudios, podemos analizar los modelos teóricos para detectar cual es el camino que nos puede llevar a una comprensión global del tema y plantearnos lo que falta por hacer.

La aportación de los modelos teóricos

Existe un particular interés dentro de los científicos teóricos en desarrollar modelos matemáticos para explicar la evolución de conductas como la cooperación; posiblemente porque la abstracción matemática de la cooperación y del escenario del ambiente social es más fácil de concebir y manipular de ésta manera. Se han desarrollado modelos complejos

con base en la teoría de juegos evolutivos de J. Maynard Smith y R. Price (1973) con la genética de poblaciones. En un marco general, los modelos teóricos se clasifican primero en aquellos en que la cooperación se desarrolla con beneficio directo, indirecto o recíproco (Nowak 2006; Lehmann y Keller 2006), y en aquellos de "altruismo estricto", que se desarrollan por selección familiar y efecto "*Greenbeard*" (Lehmann y Keller 2006; Sinervo et al., 2006). Estos aspectos teóricos son los que se han empleado con mayor frecuencia y los más usados para el juego matemático del modelado teórico, siendo los que incluyen la selección familiar los más favorecidos. A pesar de que la teoría de juegos evolutivos es generalmente poco realista, se han derivado conclusiones que se pueden analizar empíricamente. Por ejemplo, Santos et al., (2006, 2012), encontraron que la diversidad de interacciones entre individuos promueven conductas de cooperación, lo cual puede resultar intuitivo y practico, ya que si existe una red de interacciones diversas entre individuos, es más probable la coordinación para una estrategia cooperativa.

Los beneficios y costos se acumulan a través de las transformaciones del sistema social por los individuos. Para comprender esto, entendamos que en un sistema hay una red de interacciones que no se pueden analizar por separado, buscando los costos y beneficios individuales como lo hace la adecuación inclusiva (Hamilton, 1964). La red de interacciones sociales genera transformaciones internas en el sistema y creando un ambiente social (Powers et al., 2011). Los mismos beneficios de la cooperación pueden promover la evolución de la estructura poblacional adecuada para soportar la conducta cooperativa (Szathmáry 2011). La información aquí recuperada nos indica que el ambiente social que

perdura será aquel que logre mantener estable una conducta cooperativa de cualquier intensidad. Pero cabe considerar que dicho ambiente social es variable de acuerdo a cada sistema social, probablemente por el tipo de apareamiento y por las mismas condiciones ecológicas donde se desarrolla.

Pero ¿qué tipo de selección actúa en los ínfimos enlaces de las enmarañadas redes de una sociedad? Hasta este punto es difícil saberlo a ciencia cierta. En el estudio de la evolución social con microorganismos se dice que la selección dependiente de la frecuencia es más común en microorganismos que en metazoos, porque existe una fuerte selección, estructuración y crecimiento dependiente de la cooperación (Ross-Gillespie et al., 2007). Tal vez sea la selección multinivel una aproximación más certera, ya que provee una nueva perspectiva al problema considerando la fuerza de selección en los diferentes niveles de un sistema (Wright 2007).

Integración de enfoques en el estudio de la cooperación

Las posibilidades actuales de explorar la evolución de la crianza cooperativa se flexibilizan gracias a los avances en la tecnología de secuenciación genómica y a las décadas de estudio de la sociabilidad en diversos taxa. De esta manera, la crianza cooperativa en poblaciones naturales de vertebrados resulta apropiada para la discusión y la re-elaboración de una teoría sobre la evolución de la cooperación en los sistemas sociales. Esta revisión del tema resalta el potencial de dar una nueva perspectiva a la evolución de la crianza cooperativa. Por ejemplo, hemos visto que ante la viscosidad poblacional se crea un

sistema. Todo sistema, bajo la teoría general de los sistemas (Bertalanffy 1972), está formado por sus partes internas (los individuos), las entradas del ambiente (aspectos ecológicos y climáticos, y la migración), las transformaciones (estructura social y sistema apareamiento) y las salidas (dispersión y transmisión de experiencia). Todas estas partes forman el ambiente social y, dependiendo de sus fluctuaciones en cada una de esas partes, habrá conductas y estrategias más apropiadas. A partir esto, se puede concluir que para que ocurra la transformación de un ambiente social que favorezca la evolución de la crianza cooperativa se requieren algunas características biológicas, que resaltan por su importancia en el desarrollo de la crianza cooperativa o sistemas sociales con conductas cooperativas. Es importante que se desarrolle investigación sobre estas propiedades en poblaciones naturales y experimentales, así como en todo el espectro de vida en que existan conductas cooperativas. En seguida se listan seis de las propiedades detectadas en esta revisión:

1) Retraso en la dispersión: La cual aumenta la viscosidad poblacional. Esta puede ocurrir en primera instancia por restricciones ecológicas y de movilidad, generando una estructura genética poblacional y espacial, y aumentando el parentesco entre individuos.

2) Relación genética: en la cual aumenta la probabilidad de que haya alelos comunes en mayor frecuencia dentro de los grupos familiares y en el conjunto de las partes de la unidad social. Esta puede ser causada en parte por el retraso en la dispersión.

3) Variación temporal y espacial de la viscosidad poblacional: es decir variación en la

composición y tamaño de la unidad social, que en un tiempo ecológico pueden estar relacionadas con la dinámica de fusión-fisión. Es probable que los grupos pequeños sean los que conducen a la cooperación, pues los beneficios aumentan para los cooperantes que son los portadores de la experiencia (Szathmáry 2011). En tiempos evolutivos, esto estaría relacionado con las fluctuaciones en el tamaño efectivo poblacional y la tasa de migración. Este aspecto es fundamental, ya que la diversidad de interacciones y necesidades dentro del grupo es necesaria para que exista estructura en el sistema social. Por lo tanto una población que ha permanecido estable durante mucho tiempo mantendría las mismas estrategias.

4) Heterogeneidad ambiental: esta permite que ocurra variación de la viscosidad poblacional en tiempos ecológicos y evolutivos. Además, esta generaría paisajes adaptativos robustos, que en retorno promoverían la diversificación evolutiva y la diferenciación de las poblaciones (Cooper y Lensk 2010). Esta divergencia puede estar asociada a un cambio en el sistema y estrategias sociales (Price 2008).

5) Reconocimiento parental o de coespecíficos: este mecanismo puede ser físico o conductual, como el aprendizaje asociativo, el fenotipo concordante, la locación espacial, o el reconocimiento de alelos (en el sentido de que un complejo de genes confieran un fenotipo identificable; Komdeur y Hatchwell 1999). También podría ayudar la existencia de cantos específicos aprendidos del padre o la madre (Hopp et al., 2001, Greig et al., 2012). El aprendizaje asociativo también puede estar relacionado con conductas mecanicistas que se mantienen en el tiempo; es decir rituales que le

dan cohesión a la unidad social sin importar la relación de parentesco (Price 2008).

6) Pleiotropia: esta incluye la regulación de pasos clave de la regulación genes y fenotipos, como la de la melanogénesis. La pleiotropía sería responsable de la asociación entre la base de la coloración de melanina y estrategias fenotípicas en vertebrados silvestres (Ducrest et al., 2008). Por ejemplo, en aves, los carotenoides y melaninas son empleados como señales sociales (Price 2006). La producción de melanina está asociada al sistema de melanocortinas y sus receptores, los cuales son productos postraduccionales del gen *POMC* (proo-piomelanocortin) y de otros cinco genes *MCR*s (encargados de los receptores). Además de la coloración, las melanocortinas son parte de una cascada de efectos asociados al aumento en la fertilidad y receptividad sexual en vertebrados (Schioth et al., 2005).

He terminado con el aspecto de la pleiotropia porque es un tema que con los avances actuales en genómica permitirán abordarlo con mayor precisión. Este aspecto es también clave al afectar la resolución de conflictos dentro un grupo social, al darle coherencia, cohesión y estabilidad al sistema. Si imaginamos que la pleiotropía puede ser una característica que da estabilidad a una estrategia social, puede ser la clave para desenmarañar el intrincado proceso evolutivo de la crianza cooperativa. Cabe mencionar que la perspectiva epigenética también puede explicar e integrar algunas respuestas fenotípicas ante las restricciones ambientales. Faltaría saber qué fuerzas evolutivas han actuado sobre genes con efecto pleiotrópico y si el polimorfismo responde a la heterogeneidad del ambiente y del ambiente social. En este sentido es importante resaltar que la pleiotropía no puede ser

vista como la causa determinante de la expresión de la crianza cooperativa, pero sí como el efecto epigenético de la conducta y el ambiente social.

Tabla 1: Glosario

Selección de grupo: Proceso mediante el cual se favorecen las estrategias sociales beneficiosas para los grupos sociales, debido a que los individuos son dependientes de la estructura social de los grupos, y los grupos son dependientes de la estructura de la población local formada por los grupos vecinos (Wilson 1975).Este modelo ha sido extendido y actualmente se llama selección multinivel (Wilson y Sober 1994)
Selección familiar: Proceso mediante el cual se favorecen las estrategias y los individuos que las expresan por tener un efecto beneficioso en la adecuación de un pariente (*Kin selection*) (Hamilton 1964).
Viscosidad poblacional: Es una característica de las poblaciones que se encuentran con una limitante de dispersión que aumenta la relación genética entre vecinos (Wilson 1975).
Dispersión budín: Dispersión de individuos en grupos en una dimensión estructurada. Se le llama budín porque figurativamente se ejemplifica como un budín con pasas, donde los grupos son las pasas distribuidas en un medio con cierto grado de "viscosidad" (Wilson 1975).
Adecuación inclusiva: Es la adecuación de un individuo expresada por la relación genética y la adecuación directa e indirecta. Ocurre por el efecto de las acciones individuales en el éxito de la progenie de un pariente genético y por lo tanto en la adecuación clásica del individuo (Hamilton 1964).
Altruismo: Conducta costosa para el actor y benéfica para el que la recibe. El costo y beneficio son definidos en la duración del efecto de la conducta en la adecuación directa del individuo que la expresa (Hamilton 1964).
Cooperación: Conducta que provee un beneficio a otro individuo diferente al que la expresa (Lehmann y Keller 2006).
Sistema social: El sistema social de una especie está formado por la organización (composición del grupo, solitario o grupo familiar), el sistema de apareamiento y la estructura social (descripción de las interacciones entre individuos) (Kappeler y van Schaik, 2002).
Variación intraespecifica de un sistema social: Diferencias en algún aspecto del sistema social en diferentes unidades sociales o poblaciones de una especie. Debe tener una base genética de tal manera que dos poblaciones al seguir estrategias alternativas se pueden llegar a diferenciar genéticamente, sobre todo si involucra diferencias en el sistema de apareamiento (Lott 1991).

Pleiotropia: Del griego pleio="muchos", tropia= "afecta". Fenómeno a través del cual un solo gen afectas múltiples fenotipos que aparentemente no están relacionados. Los cambios que ocasiona ese gen pueden ser sustanciales para el organismo. Estos cambios pueden ser cualitativos y a lo largo de la evolución pueden ser seleccionados por la correlación del gen responsable a múltiples rasgos fenotípicos (Lobo 2008)
Melanocortinas: Hormonas peptídicas (como la hormona estimulante de los melanocitos, MSH) que actúan en cinco receptores relacionados con la expresión de la producción de pigmentos de melanina en la células de la piel en vertebrados (Schioth et al 2005).
Efecto epigenético: Modificaciones moleculares con potencial heredable que altera patrones de expresión genética sin alterar la secuencia del DNA (Carey 2011).
Teoría del juego evolutivo: (Evolutionary Game Theory, EGT por sus siglas en inglés). Formalizada por J. Maynard Smith y R. Price en 1973, es la aplicación de un juego teórico donde se enmarca el contexto, el análisis y los criterios matemáticos para predecir la prevalencia de estrategias competitivas.
Estrategia Evolutivamente Estable: (Evolutionary Stable Strategy, ESS). Una población donde todos los individuos tienden a tener la misma estrategia fenotípica y es mantenida por selección natural (Maynard 1972).
Regla de Hamilton: El gen de la conducta social "altruista" se favorece por selección natural si la suma de la relación genética "r", el beneficio "b" y el costo "c" es mayor a cero (Hamilton 1964).
Subsocial: Cuando un organismo tiene conductas de cuidado parental, como puede ser la madre hacia su progenie (Eberhard 1975).
Efecto "Greenbeard": Donde se favorece el altruismo entre parientes no genealógicos, a través del reconocimiento de una característica fenotípica compartida, como la coloración, y por la carga genética del mismo alelo relacionado (Lehmann y Keller 2006; Sinervo et al 2006).

CAPÍTULO II: Variation in the social organization of the Yucatan jay (*Cyanocorax yucatanicus,* Dubois 1875) along an environmental gradient

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Introduction

Environmental constraints and temporary variations of climatic phenomena affect the social systems in birds (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011) as they have an important influence over seasonally restricted reproductive activities (e.g., when parents begin their egg-laying they maximize food availability for fledglings (Both, 2011)). Therefore, any environmental alteration that affects the resources and their periodicity requires an adjustment of birds' social behavior during the reproductive season. Natural populations of cooperative breeding birds characterized by alloparenting behavior (Skutch 1935; Brown 1987; Koenig and Dickinson, 2004) offer an opportunity to understand the influence of environmental constraints on social systems. Cooperative breeding in birds has been explained as an adaptive strategy for inter-annual fluctuations in highly variable environments, as it allows for a successful reproduction in both difficult and advantageous years (Rubenstein and Lovette 2007). This hypothesis has been invoked to explain the

evolutionary patterns of cooperative breeding at the genus and family levels in birds (Rubenstein and Lovette 2007). For instance, Edwards and Naeem (1993) considered that, social aspects such as group size, are unstable factors to uncover a phylogenetic signal. At the species level, spatially variable climatic factors can influence the size of social groups (Brown and Horvath 1989; Edwards and Kot 1995; Bhagabati and Horvath 2006, Zöttl et al., 2013). This influence has been associated with latitude and ecological variables responding to spatial patterns, as observed for group size-aridity co-variation in populations of *Pomatostomus temporalis* (Edwards and Kot 1995).

Variation in group size in cooperative breeders like many jays can be predicted by several factors such as elevation, vegetation type and plumage ontogeny (e.g., in *A. ultramarina;* Bhagabati and Horvath 2006), thus implying an interconnection between history and ecology (Brown and Horvath 1989). According to Lott (1992) the intraspecific variation of social systems may be influenced by the delayed dispersal of members of a given group, while Zöttl et al., (2013) stated that group size could increase the fitness of its members in relation to environmental factors. Besides, Rubenstein (2007) and Canestrari et al., (2012) considered that the age and gender composition of a group may be also relevant for changes driven by environmental constraints (Rubenstein, 2007; Canestrari et al., 2012). Therefore, intraspecific variations in social systems against different environmental conditions may be highly informative to understand the behavior adjustments in group size and age composition (Lott 1991; Edwards y Kot 1995; Bhagabati and Horvath 2006; Zöttl et al., 2013).

Raitt and Hardy (1976) and Peterson (1991) reported that there was a significant group

size variation within the *Cissilopha* assembly, with an especial emphasis on differences between *C. sanblasianus sanblasianus (19 individuals)* and *C. s. nelsoni (4.5 individuals)*. Although they did not perfomed a formal analyses to evaluate the significance of such variation on an environmental context; for instance by comparing group size changes along ecological gradients. The Yucatan jay (*Cyanocorax yucatanicus*) is a cooperative breeding bird belonging to the above *Cissilopha* assembly (Raitt and Hardy 1976) and endemic of the Yucatn Peninsula in southeastern Mexico and norhtern Central America. It inhabits a wide range of heterogeneous habitats across the peninsula (Howell and Webb, 1995) and exhibits morphometrical geographic variation among extreme populations (Chablé 1999). Two phases with changes in their social organization have been described along the reproductive seasons (Raitt and Hardy 1976). These include the pre-reproductive phase, groups compound just by adults and subadults (from the end of the winter and during spring) and the reproductive phase that include the juveniles or fledglings in the groups, at the beginning of July to November (all the summer and the beginning of the winter (Raitt and Hardy 1976). These characteristics make the Yucatan jay a useful model to analyze the intraspecific variation of social organization and its relationship with environment.

In this study, we analyzed the relationship between the social organization (group size and age composition) of the Yucatan jay according to its location along an environmental gradient describing both phases of the reproductive season. We suveyed the social organization during two consecutive reproductive seasons (2012-2013), and used two climate databases to discover putative relationships with environmental constraints. We aimed to shed light on

the significance of geographic variation of social features (as an adjustment to environmental conditions), to provide new evideen for the importance of these associations in plastic behavioral traits in natural bird populations.

Material and Methods

Study area

Weather types (Köppen system) in the Yucatan Peninsula (N21˚30´, W92˚30´) are mainly determined by rainfall patterns. The Peninsula is characterized by large plains (with an average altitude less than 100m) with some scattered raising plateaus (250-350 m) in the south (Hubp and García-Arizaga 1999; Vázquez-Domínguez and Arita 2010). A climatic gradient with a northwest - southeast direction divides the peninsula in two regions (Duno-de Stefano et al., 2012) due to changes in precipitation and humidity (Howell et al., 1995). The peninsula is also affected by a double sea-breeze originated by variations in global temperature, including the El Niño Southern Oscillation (ENSO) (Gunn et al., 1995; Gunn et al., 2000). This gradient generates floristic changes, resulting in tropical dry forests (TDF) in the northwest; tropical subdeciduous forests in the central area (TSDF), and tropical evergreen forests (TEF) in the humid southeast region (Rzedowski, 1990; Figure 1).

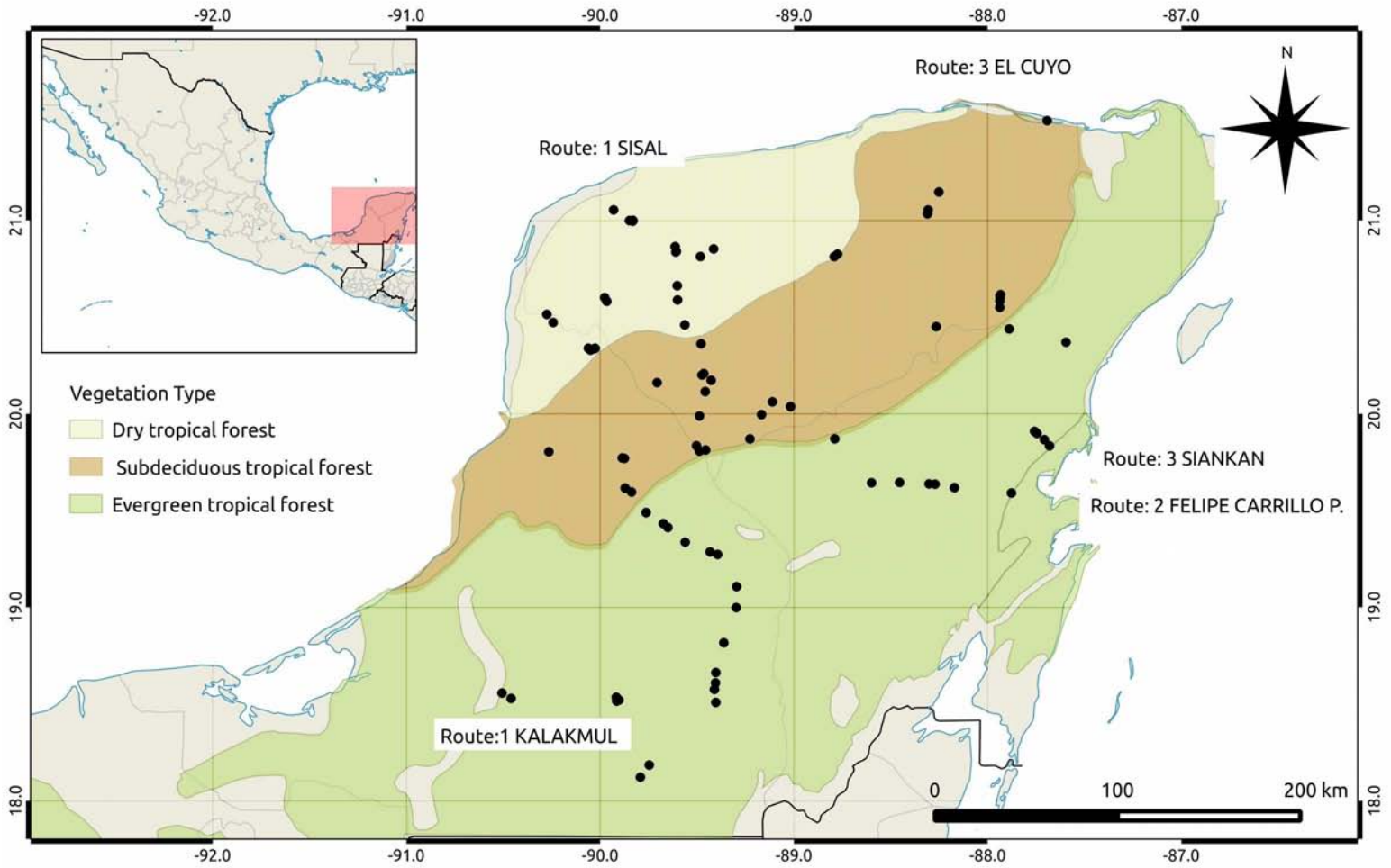

Figure 1. Social groups of the Yucatan jay over the three routes sampled and the three vegetation types of the Yucatan Peninsula according to Rzedowski (1990). Route 1: Sisal - Kalakmul (“La Ruta de los Chenes”); Route 2 : Sisal - Felipe Carrillo Puerto ("Ruta Pucc"); Route 3: El Cuyo - SianKan.

Environmental gradient

We evaluated environmental conditions of the peninsula using two climatic databases to predict the social organization of the Yucatan jay. First, eighteen bioclimatic layers were downloaded from WorldClim (Hijmans et al., 2005; www.worldclim.org) includning mean, maximum, minimum and range values for precipitation and temperature (the altitude variable was excluded from the analysis because this is a flat area). A principal component analysis (PCA) was then performed to reduce the number of correlated variables. The first four PCs, explaining 94% of the climatic variance, were retained for further analyses. The second climatic database was a fine-scale set of environmental variables from 460 climatic points distributed along the peninsula. It was downloaded from the Mexican National Meteorological Service (add website location here). It included monthly and annual rainfall data for 91 years (1920 to 2011), which were used to analyze the temporal patterns and fluctuations of precipitation by using with Colwell's (1974) indexes. Contingency and constancy indexes were employed to obtain the degree of rainfall predictability index, which is associated to the seasonal patterns of flowering and fruit availability in tropical trees (Colwell 1974). This two variables are assumed to be crucial for initiating the reproductive season of the Yucatan jay.

Constancy measures year-to-year the stochastic variations in temporal patterns (i.e., temporal variability), contingency measures the degree of the seasonal pattern repeated within each year (i.e., seasonality), and predictability, is the sum up of the last two indexes, that is the uncertainty of occurrence between time and season. The analysis for the climatic data and modeling were done on R 3.0 and Perl 5.16.3. Specific illustrations showing the

environmental gradient (Figure 5 and 6) were obtained with an Inverse Distance Weighting (IDW) interpolation in QGIS 2.0 (2013) using the bioclimatic variables and the Colwell indexes mentioned above.

Social organization (group size and composition)

Detection and registering of each member of every social group was facilitated by the fact that Yucatan Jays (as most corvids; Baglione et al., 2002) forage, move and defend their territories together..Social organization data were obtained during the reproductive seasons from March to August (2012 and 2013). Briefly, following Raitt and Hardy (1976), we divided observations in two phases: from April 1st to May 30th, to detect *pre-reproductive groups* (without juveniles), and from June 1st to July 30th, to identify *reproductive groups* (with juveniles). Three federal routes and several dirt roads were surveyed (Bibby et al., 2000; Figure 1): Kalakmul - Sisal (through the “Chenes Route”), which runs from south to north over the west side of the peninsula; and Sisal - Felipe Carrillo Puerto, and Sisal - Sian Kan (passing through "El Cuyo"), which cover the northwest and the southeast portions of the peninsula. We followed the Brown and Brown (1985) and Brown and Horvath (1989)’s methods, and sampled along each route from 6 to 11 am and from 4 to 7 pm. At the beginning of each route, we took a slow walk for 1km during 30min, and made our recordings as soon as a group was found. To avoid overlapping or double counting social groups, we drove 1.5 km after each recording (Figure 2). The social composition was determined by visual

examination (using 10x42 binoculars) according to the age phenotypes described by Hardy (1973; see Fig. 3).

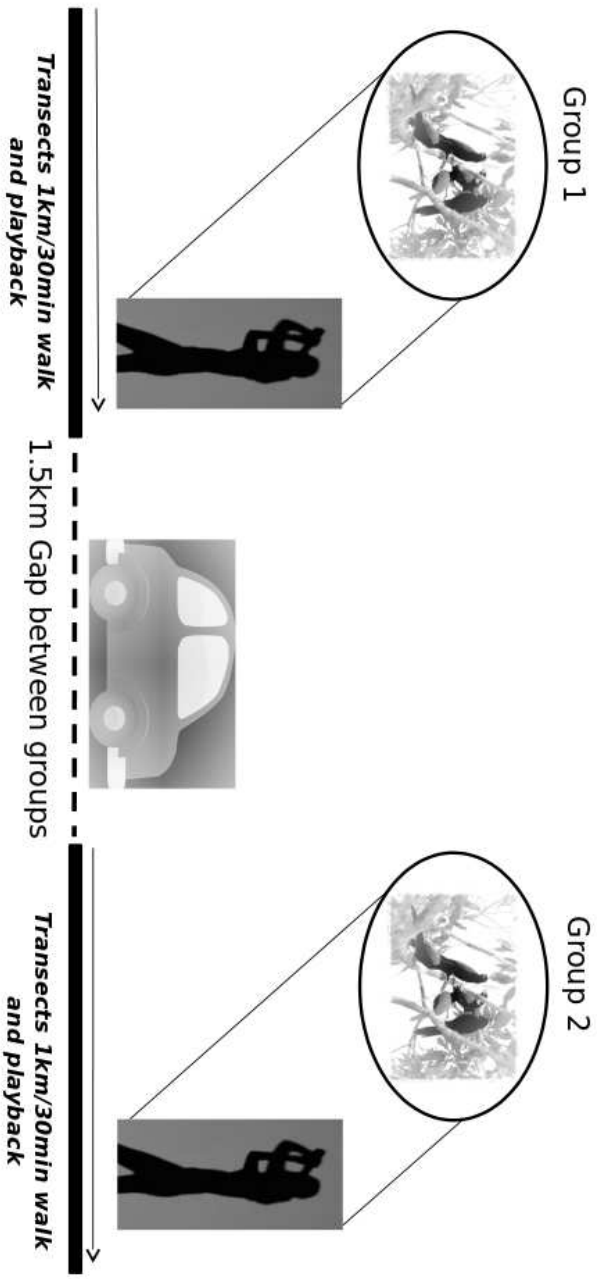

Figure 2. Sampling method to detect the Yucatan jay social organization (group size and age composition). Transect represent one sampling area to detect one group and transects follow the three existing routes federal and dirt roads, with a gap of 1.5 km car drive between groups.

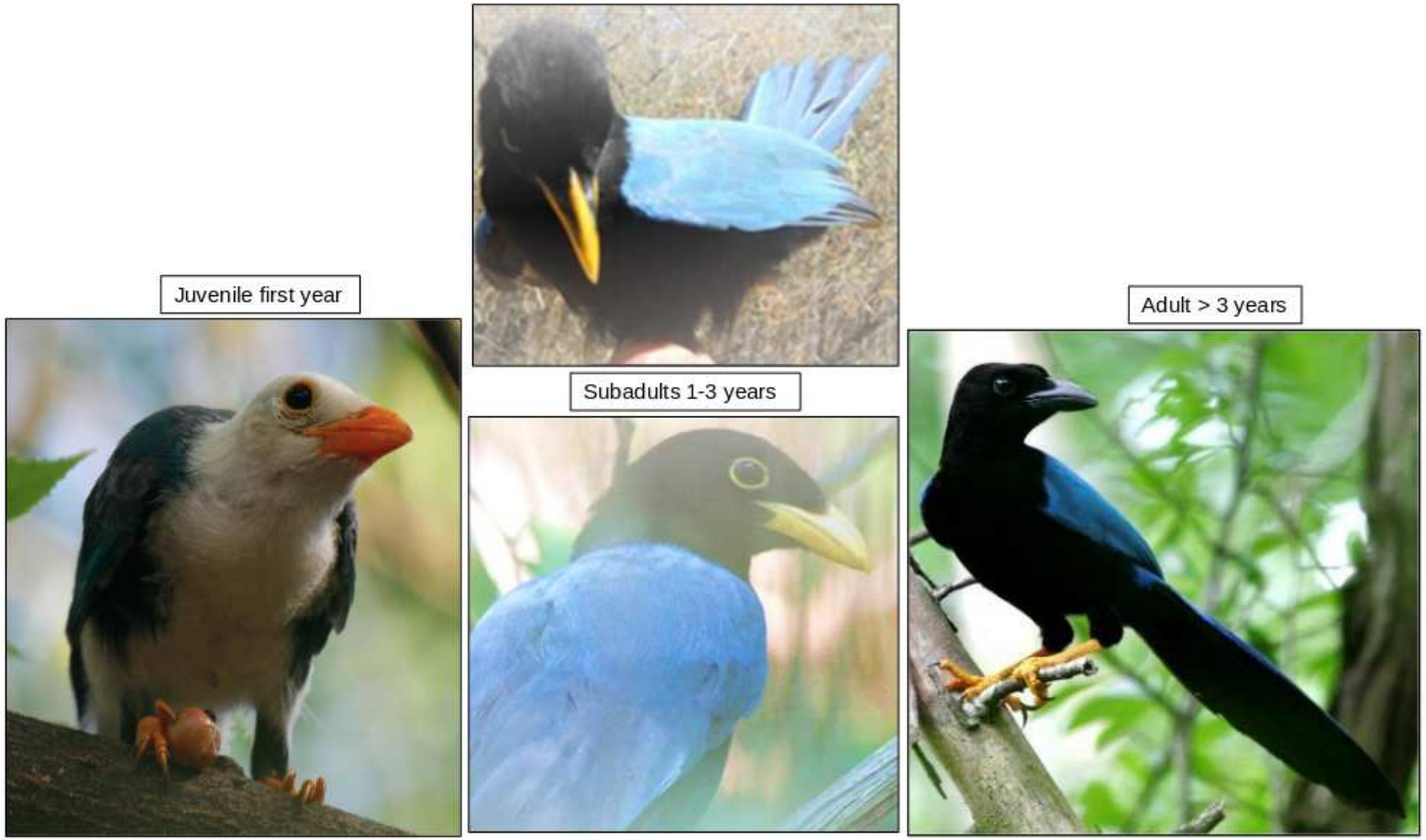

Figure 3. Age phenotype classes proposed by Hardy (1973) for the Yucatan jay.

Data analysis

Routes and social groups were drawn on a map and overlapped on the potential vegetation types reported by Rzedowski (1990) (Figure 1). Sampling distances, together with the location of social groups and climatic stations were also displayed on this map. An analysis of variance (ANOVA) followed by a Tukey HSD test was performed between the different types of vegetation and social groups to infer differences in social organization. A t-test was also done to detect differences in social organization between the two phases (pre-reproductive and reproductive) and years (2012-2013) for each vegetation type and for the complete species' range.

The dependence between social organization and the environmental gradient was analyzed with a Generalized Linear Model (GLM), using the fourth PCs explaining the climate variance (in the PCA analysis) as independent variables to avoid co-linearity. Because the Colwell's indices are interdependent, we also carried out independent Linear Models (LM) with each index to detect the relationship between climate and social organization. All statistical analysis was carried out in R 3.0, with an alpha value < 0.05.

Results

Environmental gradient

The environmental gradient recovered from the WorldClim layers showed that the annual mean and warmest quarter temperatures were the most significant ones explaining more than 94% of the variance in the PCA (see in Appendices Figure 1 and Table 1). Two climatic clusters were distinguished at the PCA plots respectively conformed by the dry and evergreen forests, with the subdeciduous forest locations scattered between them. The PCA interpolation showed a warm patch in the northwest, coinciding with the TDF location, and a cooler one in the southeast and the northeast, where most of the TEF is located (Figure 4). Nevertheless it most be noted that temperature differences between these two extremes were less than 10°C. A similar pattern was recovered with the Colwell's index, where interpolations showed that the southern region had the highest index values in rainfall predictability and constancy. The contingency index revealed that both the north and the south had higher values than the central region (Figure 5).

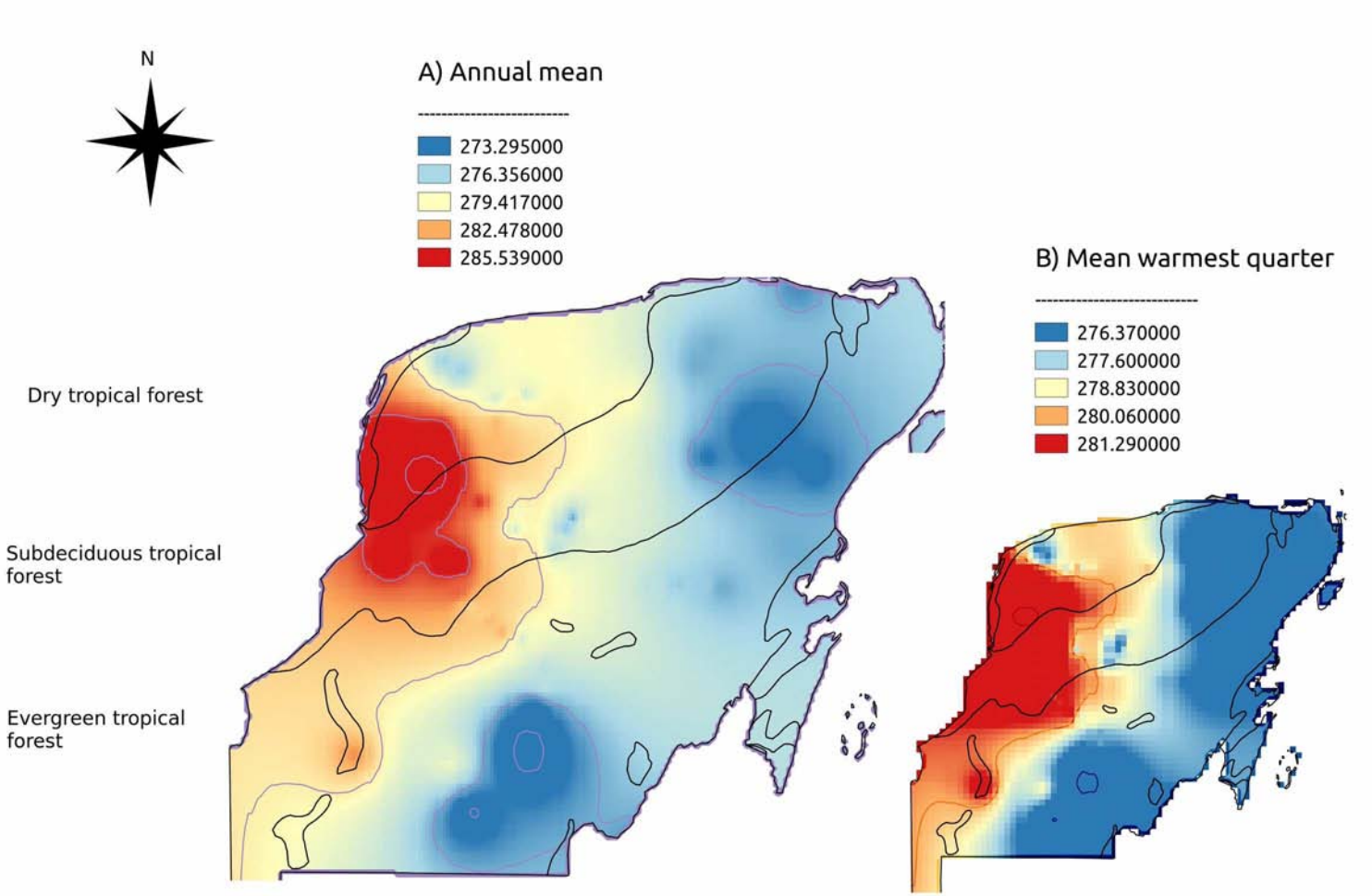

Figure 4. Inverse Distance Weighted interpolation (IDW) of annual mean temperature (A) and mean temperature of warmest quarter (B) at the Yucatan Peninsula in the three vegetation types.

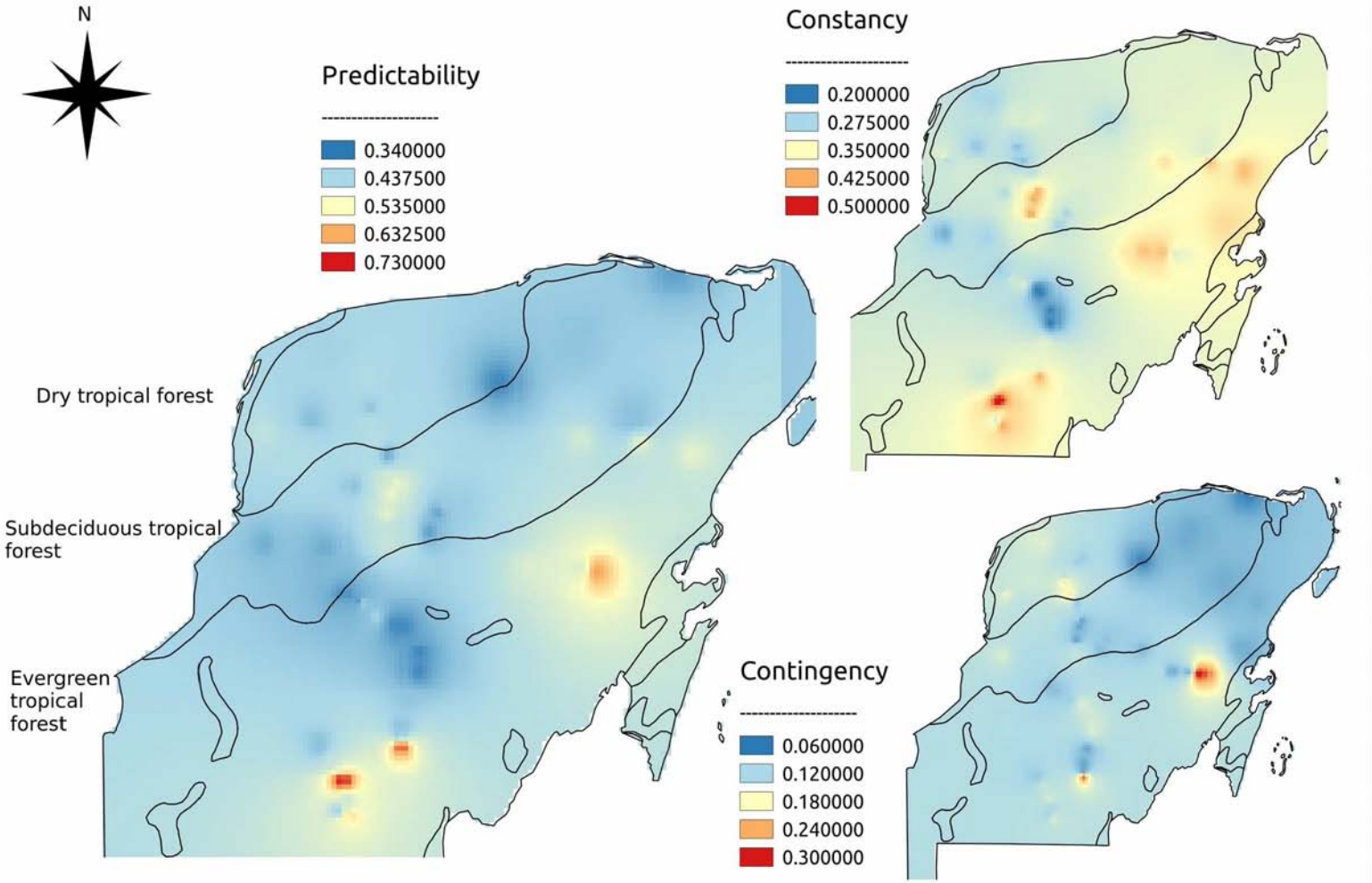

Figure 5. Inverse Distance Weighted interpolation (IDW) of rain fall predictability (A), constancy (B) and contingency (C) at the Yucatan Peninsula in the three vegetation types.

Social organization in the environmental gradient

We covered around 1000 km per year and phase to collect information about the Yucatan jay social organization, including a mean of 302.6 km per vegetation type and phase per year (Table 1). In total, we registered 93 *pre-reproductive* groups (46 and 47 in 2012 and 2103, respectively) and 47 *reproductive* groups (34 and 14 groups each year) during the two seasons surveyed. In 2013, due to an abnormally intense drought in the northern region the number of reproductive severely diminished. This reduced in some ways our statistical power to compare *reproductive* groups between years. However, we consider this a relatively minor issue given that no significant relationships were observed between the *reproductive* groups' features and the environmental gradient variables for the more adequately sampled year 2012 (see in Appendices Table 4).

For the *pre-reproductive* phase, the ANOVA followed by Tukey HSD tests showed differences in group size and number of subadults between the dry and the evergreen forests (see Figure 6(A) and in Appendices Table 3). Differences between phases were also detected for these two variables (Figure 6(B)) but only within the evergreen (group size t = -2.6568, df =16.317, p-value = 0.01702; subadults t = -3.0843, df = 16.55, p-value = 0.006892) and subdeciduous forests (subadults t= -2.4788,df= 19.613,p-value= 0.0224) (see in Appendices Table 2). Differences between years (see Figure 6(C)) of data collection were just in the number of subadults at the evergreen forest (t= -2.905, df= 28.25, p-value= 0.007061), and the number of adults at the subdeciduous forest (t = 2.4335, df= 19.713, p-value= 0.02461). No differences between phases or years were observed in the dry forest (see in Appendices

Table 2).

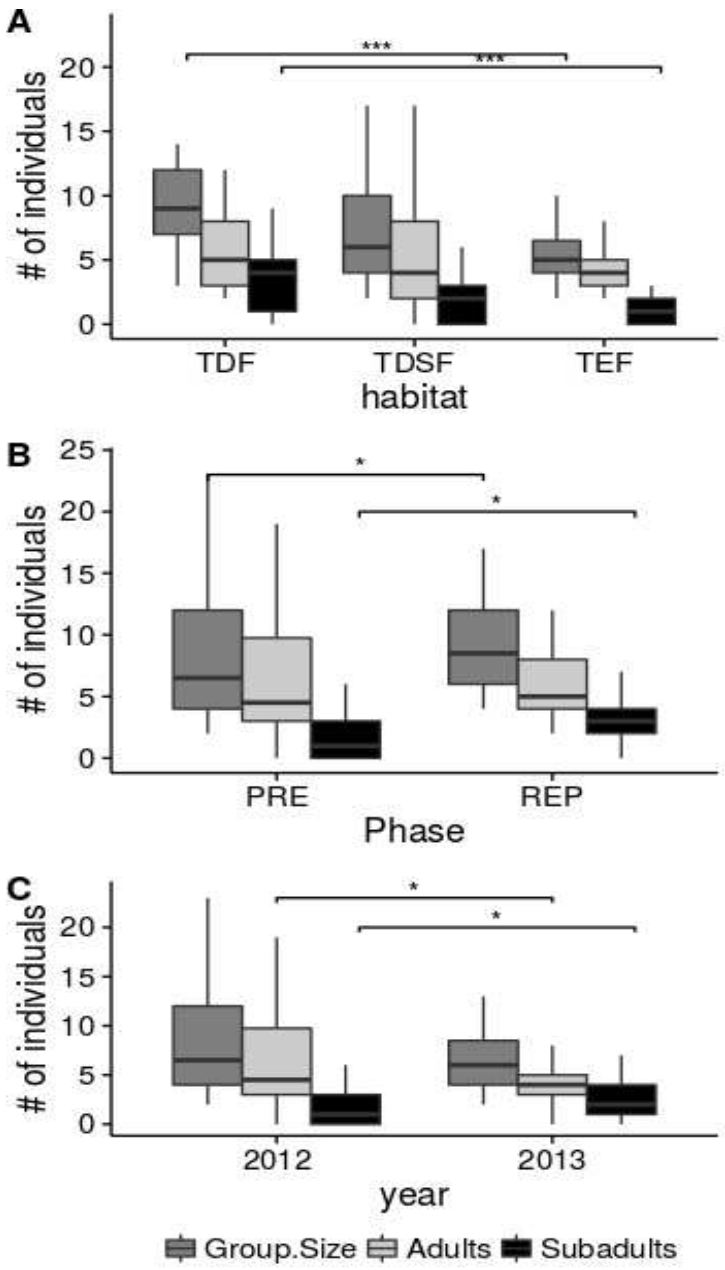

Figure 6. Yucatan Jay social organization (Group size, subadults and adults quantity). Statistical differences between; A) Each vegetation type at the Pre-reproductive phase, TDF=Dry tropical forest, TSDF=Subdeciduous tropical forest and TEF=Evergreen tropical forest; B) Phases PRE= pre-reproductive and REP = reproductive; C) Years at the pre-reproductive phase (2012-2013). Boxplot contain extreme of the lower whisker, the lower 'hinge', the median, the upper 'hinge' and the extreme of the upper whisker.

The GLMs performed with four outcome variables (the first four PCs from the bioclimatic PCA), showed a significant and positive prediction of group size in the *pre-reproductive* phase (see in Appendices Table 5). The mean annual and warmest quarter temperatures were the most significant predictors of group size (respectively, Figure 7(A) and Figure 7(B)). The LM models further showed that the number of subadults per social group was the only significant social feature that could be related to the environmental gradient, most particularly with the rainfall constancy index (see in Appendices Table 6). For instance, regions with low and intermediate constancy index had the highest retention of subadults per group. Locations with extreme constancy values at their turn showed a lower number of subadults (Figure 7(C)).

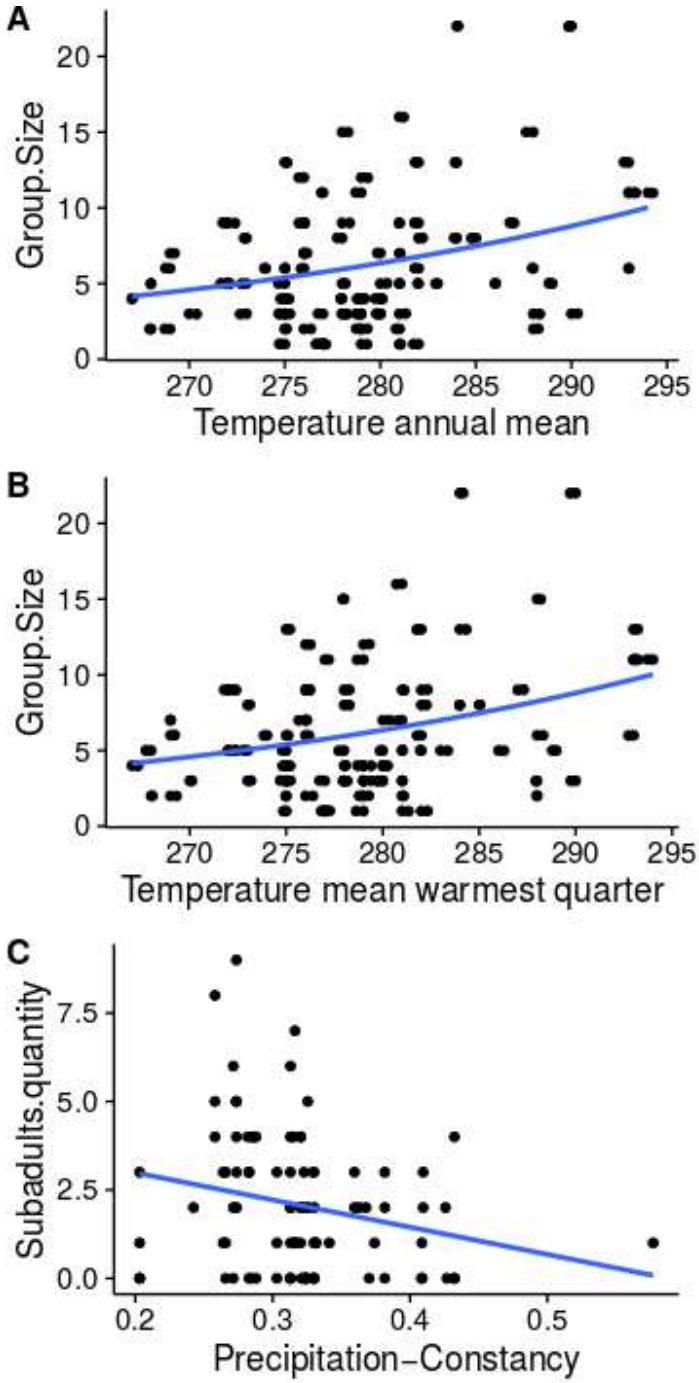

Figure 7. GLM and LM Regression plots of Yucatan Jay social organization predicted by environmental conditions. A) Group size predicted by annual mean temperature (GLM); B) Group size predicted by mean warmest quarter temperature (GLM); C) Number of subadults predicted by precipitation constancy index (LM).

Discussion

In this study, we found that the social organization of the Yucatan jay varies with the types of vegetation across the Yucatan Peninsula, and that such changes can be predicted by temperature and rainfall constancy. Even if the regression analyses still need to be fine-tuned with long-term data, the relationship observed herein shows that jays can adjust their social system to temporal and environmental conditions. Group size and the number of sub-adults remaining in the group are among the most important social features related to the environmental constraints in the Yucatan Peninsula. It is important to emphasize that the previously described *reproductive* and *pre-reproductive* phases (Raitt and Hardy 1976) could be clearly differentiated between the three vegetation types. These might imply that the fusion-fission dynamics work as an adjustment of the social traits to environmental constraints and, could also be important to detect intraespecific social variations in future in this species.

While differences in social organization according to vegetation type were found between extreme populations, the central region acted more like an ecotone; it shows characteristics of both the dry and the evergreen forest. In the southern and more climatically predictable evergreen forest, the Yucatan jay forms small family groups with few subadults (probably belonging to the penultimate generation), implying a lower delay in dispersion. However, in the northern (and less predicatable) dry forests, groups are composed by more individuals, especially subadults (probably including by more than three generations), which should result in a higher delay in dispersion. Differences in group size and composition were detected between habitats during the *pre-reproductive* phase, while differences within

habitas, particularly within the evergreen forest, were observed between both phases (*pre-reproductive* and *reproductive*). This happens at the fledgling breeding phase where the unsuccessful groups associate with neighboring ones (Raitt and Hardy 1976). Then, a fission of these large groups is expected at the next pre-reproductive season.

This kind of fusion dynamics had already been seen in other groups of birds with cooperative breeding (Baglione et al., 2002, et al., 2006; Griesser et al., 2009), and it is relevant aspect to distinguish the more cohesive social groups from the less cohesive ones. The first groups should have a more limited dynamics and the last ones, which should be more flexible in their composition, the integration of new members is easily accepted (Aureli et al., 2012). Our results suggest a more cohesive social system in the Yucatan jays populations from the dry forests (no differences between phases), in contrast with from the evergreen forests. Could be interesting to analyze in future studies the paternity and kin structure with genetics tools, to distinguished between these to populations in relation to the social dynamics. We will expect a high kin structure and close paternity relations in the north populations were the social fusion-fission dynamics seams to be more cohesive for the Yucatan jays.

Our results further suggested that the rainfall constancy index is a significant predictor of the size and composition of social groups, and thus to infer the delay in dispersion of subadults. These individuals seem to assemble in social groups that inhabit regions with low constancy index (but up to 0.2 constancy index), and thus more unpredictable climates from one year to the next. The indexes employed herein have been shown to be associated with

patterns of seasonal flowering and fruit-bearing in tropical trees (Colwell 1974), which are crucial for a correct progression of the reproductive season. From this point of view, a lack of constancy of rainfall between seasons might prompt the subadults to delay their dispersion. Furthermore, in less predictable environments (i.e. where parents lay eggs without guaranteed food availability), the role of subadults might be relevant for alloparenting and the success of the social group as whole (with a subsequent increased size).

For instance, we found limitations for comparing the social organization of the *reproductive* phases between the two years surveyed due to a delay in egg-laying in 2013. This year, an intense drought hit the Yucatan Peninsula, more particularly in its northern portion, at the beginning of the reproductive season, which translated in a 150-175% anomaly rainfall rate (Encarnación et al., 2013 SMN annual report). Such climate instability, across years, may result by a worldwide phenomena as “El Niño”. Probably, these kind of phenomena could be provoking the constancy differences on precipitation across the Peninsula. Hence, as we mention this might affect the subadults decision to remain on the social groups, at the less constant region of the peninsula. For a better understanding of the development of cooperative breeding, as the contribution of subadults along an environmental gradient is decisive.

Group size adjustments to the social organization in birds have been previously detected across changes in elevation, vegetation features *i.e.* tree height (Bhagabati and Horvath 2006; Langen and Vehrencamp 1998), latitude, and aridity (Edwards and Kot 1995). Even if Edwards and Naeem (1993) have considered that group size is an phylogentically

unstable feature; at the species level, major group size variation have been detected between jay populations (Brown and Horvath 1989; Peterson 1991). Some authors have argued that these adjustments imply a dual role between history and ecology (Brown and Horvath 1989), as are the cases between *A. ultramarina couchii* and *A. ultramarina arizonae (*Brown and Horvath 1989), or between *C. sanblasianus sanblasianus* (19 individuals *per* group) and *C. sanblasianus nelsoni* (4.5 individuals *per* group) (Peterson 1991). We proposed that similar processes may be occurring in the Yucatan jay between the dry and the evergreen forest populations. Based on the geographical comparison and the scales of analysis used on this study, it should be interesting to verify if the social organization differences of the Yucatan jay in relation to vegetation type also translate on adaptations to climate and habitat type. A genome scan performed by our points in that direction, as SNPs associated to particular genes revealed similar associations with vegetation type than those observed at the social group level (Termignoni-García et al., 2016 on revision). Whether there is a causal correlation between these two aspects remains a task for future studies aiming to explain the geographic variation and microevolution of this species.

In conclusion, this study work reinforces the idea that jays are candidate species to investigate the associations between ecological factors and social behavior. We provided new information to evaluate the significance of social organization for geographical variation using social traits in bird populations. This study further suggests that intraspecific changes in the social system may be an adaptation to different environmental conditions, and may have a possible implication in population divergence and incipient speciation processes.

Capítulo aceptado en la revista Molecular Ecology

CAPÍTULO III : Genomic footprints of adaptation in a cooperatively breeding tropical bird across a vegetation gradient

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Introduction

Disentangling the genetic basis and evolutionary drivers of phenotypic variation is one of the central objectives in evolutionary biology. Given that selection generally operates on phenotypes (reviewed in Kingsolver et al., 2001), it is commonplace to believe that most phenotypic variants have an associated adaptive value, and that they evolve and are primarily maintained by ecologically-driven selective forces (Newton 2003). However, many examples

exist suggesting that significant phenotypic differentiation may arise by genetic drift or patterns of relatedness within or among populations or species (Zink & Remsen et al., 1986; Campagna et al., 2015; Gray et al., 2015), or can result from phenotypic plasticity across populations (Mason & Taylor 2015). Furthermore, when populations are not effectively isolated from each other or when they are arranged across environmental gradients that may influence phenotypic variation, they can conform to patterns of isolation by distance and/or adaptation, two outcomes that are sometimes difficult to distinguish from each other (reviewed by Forester et al., 2016). In addition, given that most phenotypic variation is produced by the interaction of alleles at multiple loci and that different allelic combinations can sometimes result in similar phenotypes, pinpointing individual candidate loci may be complicated, especially for non-model species (e.g. Gray et al., 2015).

The development of high-throughput sequencing is revolutionizing evolutionary biology and expanding the conceptual framework of molecular ecology (Keller 2014; Andrew et al., 2013; Edwards et al., 2015). For instance, it has permitted easier distinction between neutral and putatively adaptive processes in the genome (Frichot et al., 2013; Lotterhos & Whitlock 2015 ; Gautier, 2015), making clearer the association between phenotype and genotype variation under a range of environmental conditions. It has also begun to shed light on some of the molecular and physiological processes underlying specific adaptations (e.g. Kirk et al., 2011, Rellstab et al., 2015., Günther et al., 2013; Manthey & Moyle 2015). Likewise, recent methodological and statistical advances have improved the ability of such studies to pinpoint specific genomic regions implicated in local adaptation and measure their contribution to the

total adaptive variance of a population or species (reviewed in Rellstab et al., 2015).

Over the last decade, since the publication of the complete chicken genome (Hillier et al., 2004), bird genomics research has significantly advanced (reviewed by Kraus et al., 2015). For instance, it is now known that the genomes of birds are highly syntenic and conserved at both the nucleotide sequence and chromosomal structure levels (Ellegren, 2013; Zhang et al., 2014; Gossmann et al., 2014; Jarvis et al., 2014), and that the efficiency of selective forces (and the incorporation of new beneficial mutations) within and between species is mostly modulated by the highly variable recombination rates across these genomes, than by intrinsic factors inherent to each independent taxa (e.g. Gossmann et al., 2014; Burri et al., 2015). This opens the door for further studies, particularly in non-model bird species. For example, the first feature allows the use of the available bird genomes to guid*e* *mini-contig* building and SNP discovery in non-sequenced species (e.g. Lemmon et al., 2012; DaCosta & Sorenson 2016), while the second encourages new empiric searches for convergent molecular signatures of local adaptation, which at some point will allow further genomic comparisons at higher taxonomic levels (e.g. Jarvis et al., 2014).

The Yucatan Jay was classified as a cooperative breeding bird, territorial, plural breeding with separate nest (for the two pairs in unit) and where yearlings feeds the young and delay breeding for 2 or more years (Brown 1987; Raitt et al., 1976). Similar to the reproductive system of *Aphelocoma ultramarina* and *Gymnorhina tibicen* (Brown 1974, 1978, 1987). Also is distributed across an environmental gradient mainly driven by northwest - southeast changes in precipitation and humidity (Howell et al., 1995), and by responses to a

double sea-breeze effect originated by variations in global temperature, including the El Niño Southern Oscillation (ENSO) (Gunn et al., 1995; Gunn et al., 2000). This gradient further generates floristic changes across the Yucatan Peninsula, which displays tropical deciduous forests (TDF) in the drier northwest, tropical subdeciduous forests in the central area (TSDF), and tropical evergreen forests (TEF) in the more humid southeast region (Rzedowski, 1990; Figure 1). Significant morphometric variation, putatively associated with this gradient, has been reported in Yucatan Jay's populations (Chablé-Santos, 1999), and has been used to define three independent Operative Geographical Units (OGU) for management purposes (Figure 1; see also Chablé-Santos, 1999). Because the Yucatan Peninsula has no relevant geographic barriers that might hamper the Yucatan Jay's dispersal - it is mainly a large plain with only subterranean rivers and hills no higher than 350m a.s.l (García-Arizaga 1999; Vázquez-Domínguez et al., 2010)- it can be hypothesized that environmental changes might be promoting, at least partially, morphological and genetic variation in this species. For instance, vegetation differences may imply changes in food regimes, which in turn may influence morphological features related to diet across populations (e.g. Schweizer et al., 2016). Despite these gradients and morphological variation, the total geographic range of the Yucatan Jay is only ~135,500 sq. kilometers. It is one of only seven bird species endemic to the Yucatan peninsula (Arita & Vázquez-Domínguez, 2003) and provides an exciting opportunity to determine whether environmentally-induced genomic clines exist in geographically restricted species.

Heterogeneous landscapes can increse genetic differentiation between populations

independently of geographic distance (Wang & Bradburd 2014) due the influence into the gene flow (Nosil et al., 2005; Foll & Gaggiotti 2006; Thorpe et al., 2008). This isolation-by-environment (IBE) pattern is probably generated by natural selection when populations are locally adapted (Wang & Summers 2010; Bradburd et al., 2013; Wang & Bradburd 2014). Specially under strong natural selection when environmental constraints affects synchronization of mating or patterns of dispersal (Sexton et al., 2014), even in the presence of gene flow (Nielsen et al., 2009; Saint-Laurent et al., 2003; Mendez et al., 2010; Dennenmoser et al., 2014; Schweizer et al., 2016). This is a controversial issue because strong gene flow can stall local adaptation (discussed by many authors from Haldane 1930, Wright 1943 to Bridle et al., 2010) making the Isolation-by-distance (IBD) patter more common in nature (Slatkin 1993; Meirmans 2012, Wang et al., 2013). However, in natural population had been reveled that IBE its also common and explains population genetic differences in orchids (Mallet et al., 2014), fish (Dennenmoser et al., 2014), birds (Manthey & Moyle 2015) and mammals (Mendez et al., 2010; Lonsinger et al., 2015). Therfore, disentangle the relative effects of IBD and IBE its going to be an obligate task for fully understanding the ecology of local adaptation and how landscape and environmental features influence gene flow, population structure and shapes the distribution of genetic variation in nature (Bradburd et al., 2013; Wang et al., 2013; Sexton et al., 2014; Wang & Bradburd 2014).

With these ideas in mind, we used a NGS Illumina platform with paired-end sequencing of ddRAD-tag (Peterson et al., 2012) to asses genome-wide variation in the Yucatan Jay and

explore potential environmental drivers of population genetic structure. Consistent with previous studies of cooperative breeders investigated with a variety of molecular markers (Edwards 1993; Mcdonald et al., 1999; Delaney et al., 2008; Woxvold et al., 2006), we anticipated detectable geographic variation across localities, despite the small geographic distances over which we sampled birds. We used analyses associating genotype-environment and genotype-phenotype to identify candidate SNPs for adaptive processes (Frichot et al., 2013) and determine whether they conformed better to patterns of IBD or IBE. We anticipated partial overlap between candidates associated with environmental and phenotypic variation, if only because we found that environment and morphology co-varied in space.

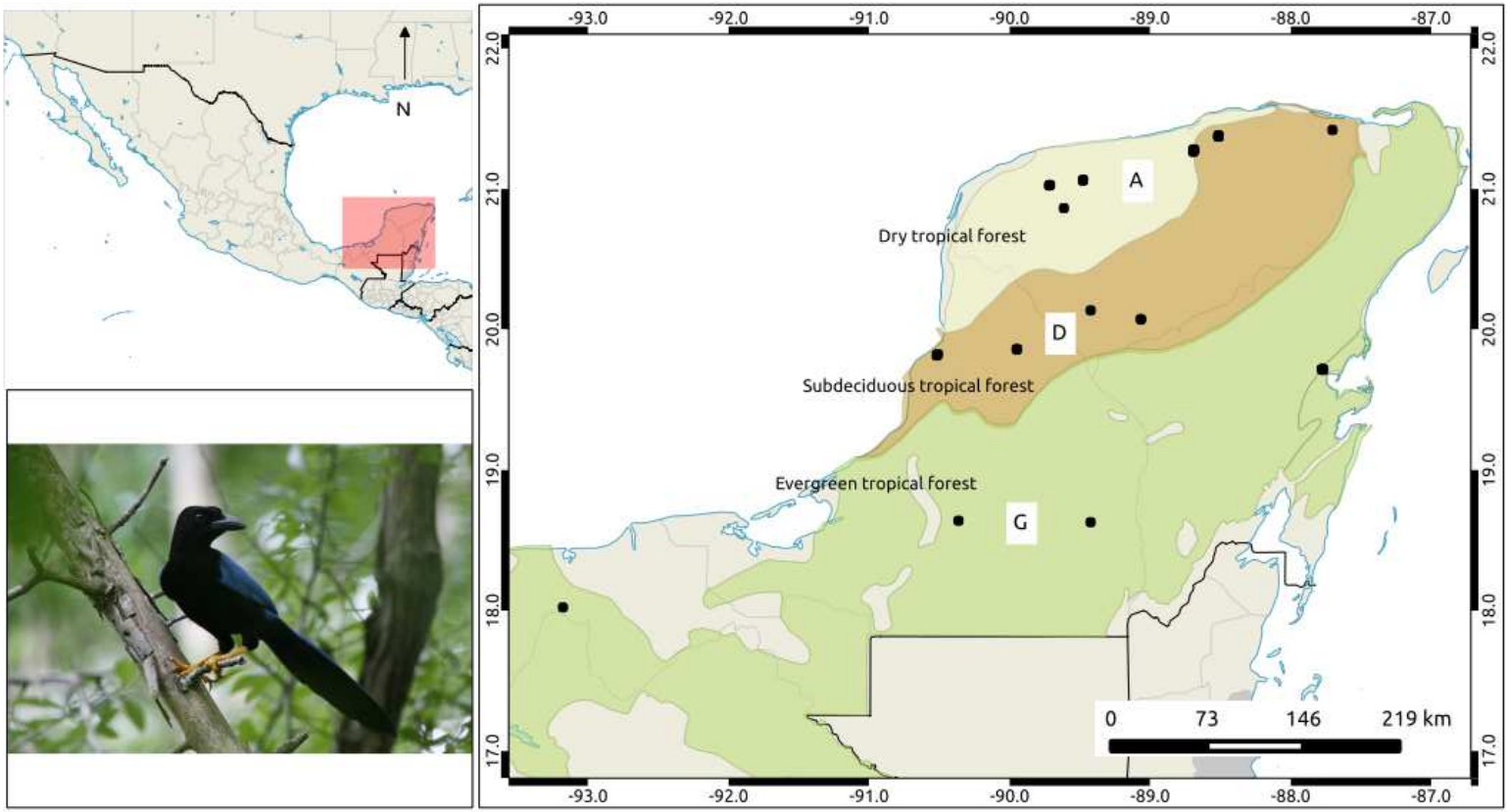
Methods

Sampling, and collection of morphological and climate data

Specimens were collected from the field in geo-referenced localities in 1996 (Chablé-Santos 1999), in total 106 individuals were sampled paying attention to minimizing the number from an individual social group. Tissues were preserved in a deep-freezer (-70°C) at the Ornithological National Collection of the Biology Institute - UNAM (CNAV); 68 of these specimens and associated tissues were selected for this study from the collection, encompassing two to eight individuals per locality, representing all three OGUs and spanning the entire range of the species (Figure 1). These specimens were selected to score

morphometric measures previously associated with geography (Chablé-Santos 1999) and to build genomic DNA libraries. Briefly, lengths for the tarsus (TRL), wing (WIL), tail (TAL), and culmen (CUL), as well as bill width (BIW) and depth (BID) were determined for each individual, taking sex into account when available. Measures were replicated ten times and averages were analyzed with a Principal Component Analysis (PCA) in R (prcomp function) to eliminate co-linearity. The first four PCs explained 84.7% of the morphological variance and were retained for further analyses (see below). For each locality represented in the set of samples, 18 bioclimatic layers, containing mean, maxima, minima and range values of variables related to precipitation and temperature, were obtained from the WorldClim database (Hijmans et al., 2005; www.worldclim.org). Also a PCA was performed in R to reduce the number of correlated variables and the first 4 PCs, which explained 94% of the climatic variance, were retained.

Figure 1. Locations of the Yucatan jay tissues selected for sequenced, along the three types of vegetation (Rzedowski 1990) and the three Operative Geographical Units (Chablé-Santos 1999); A= Dry tropical forest, D= Subdeciduous tropical forest and G= Evergreen tropical



DNA isolation and preparation of genomic libraries

Total DNA was extracted from each selected individual with the Qiagen tissue and blood kit according to the manufacturer's instructions. Libraries were prepared using the ddRAD-seq protocol (Peterson et al., 2012) standardized for birds with genome sizes similar to that of the Zebra finch and the American Crow (~1.25 pg; Peterson et al., 1994; Andrews et al., 2009). Briefly, DNA samples were digested with *Eco*RI-HF and *Sph*I restriction enzymes (New England Biolabs) and custom adapters with attached barcodes were ligated to each digested sample with T4 DNA ligase (New England Biolabs). Fragments about 345-407 bp long and cut by both enzymes (one per end) were selected with a Pippin Prep electrophoresis cassette (Sage Science), and samples were pooled on equal concentrations. A short PCR reaction of the pooled samples was performed in quadruplicate using a *Kapa-HiFi Taq* (Kapa Biosystems) as follows: an initial denaturation at 94°C for 2 min, followed by 12 cycles of 94°C for 15 s, 57°C for 30 s, and 72°C for 1.2 min, and by a final extension of 72°C for 1 min. The pooled library was tested for DNA quality and quantity with qPCR and flow cytometry in an Agilent 2100 Bioanalyzer, and sequenced in a single lane of an Illumina HiSeq2000 (Harvard Bauer Center for Systems Biology) with pair-end reads (100bp long each), yielding sequence reads for run 1 and run 2. Sequence reads were provided in two runs (run 1 and run 2), one per end, and representing restriction sites of two enzymes used.

Bioinformatic pipeline

Sequence reads were demultiplexed with the “process-radtag” routine available in Stacks v1.30. Sequences were quality-filtered with the FASTx_toolkit-0.0.12 (http://hannonlab.cshl.edu/fastx_toolkit/index.html., by Hannon Lab), and any read with a *Phred* score lower than 20 was eliminated to retain higher quality reads for SNP discovery. Retained reads were trimmed to 91 or 94 nucleotides for run 1 and run 2, respectively, with the NGSQCToolkit_v2.3.3 (Patel et al., 2012) to reduce the errors present in sequence tails (Pujolar et al., 2014). PCR clone sequences were then removed with “clonefilter” in Stacks v1.30 (Catchen et al., 2011).

Filtered pair-end reads were aligned *denovo* with GSnap (version 2014-12-17), a Genomic Short-read Nucleotide Alignment Program (Wu et al., 2010), after disabling the terminal alignments option. Because of the high genome synteny of birds (Ellegren, 2013; Zhang et al., 2014; Gossmann et al., 2014; Jarvis et al., 2014, 2014), and specifically of crows (Roslik et al., 2001), the American Crow (*Corvus brachyrhynchos*) genome assembly (NCBI assembly: ASM69197v1, accession: GCA_0006919751) was used as reference (Pseudo-Reference Genome, PRG) for mini-*contig* building and alignment. This reference and the paired-end reads available allowed for additional positioning information, thus facilitating detection rare allele variants (Peterson et al., 2012), which are often removed from *de novo* assemblies performed without a reference genome, given that they can be confounded with sequencing errors.

For purposes of comparison, sequencing reads were also assembled *de novo* without alignment to a PRG, as well as using the Zebra Finch (*Taeniopygia guttata*) as a PRG. This last alignment yielded fewer loci than the two others, and resulted in different estimates of population diversity and major allele frequencies, where as the alignments using no PRG or the American Crow as PRG had similar basic population parameters, although different in the number of final RAD-loci (Figs. S1-S6). After following recommendations by Davey et al., (2013) and Nevado et al., (2014), the best dataset and the more robust framework to recover SNPs was the American Crow PRG alignment. Parameters for this alignment included a terminal threshold of 500, a maximum number of mismatches allowed (m) of 5, and an indel penalty (-i) of 2, as recommended by Catchen et al., (2011). Sequences were then sorted by coordinates in the reference genome and optical duplicates (sequencing artifacts) were removed using picard-tools-1.119 (Wysoker et al., 2013). Finally, low quality assemblies (i.e. below 20) were eliminated with Samtools 0.1.18 (Li et al., 2009).

SNP discovery and genotype calling was performed with the Stacks pipeline v1.30 (Catchen et al., 2011) using the correction module “rxstacks”, which makes a population-based correction to genotype calling on individuals; this module facilitates removing putative sequencing errors, paralogs, and loci with low coverage from the final dataset. The reference-aligned sequences were processed with the ref_map.pl pipeline by allowing a maximum of three mismatches (n) between loci and three loci per stack (max_locus_stacks); a SNP call model upperbound of 0.05 was also used, while a maximum likelihood (lnls) value of 8 was employed for the correction module.

Population analyses

Basic estimates of population and nucleotide diversity were inferred with the populations program of Stacks v1.30 (Catchen et al., 2011). Individuals were assigned to the three OGUs (A-D and G) reported on Chablé-Santos (1999). Estimates of nucleotide diversity (π), heterozygosity (H_o and H_e), and fixation index (F_{is}) were determined from a filtered set of SNPs that included only those in Hardy-Weinberg equilibrium and with minor allele frequencies (MAF) above 0.05 within each OGU. Genetic differentiation between the three OGUs/Populations were estimated with the corrected Fst, the AMOVA Fst for each SNP recommended by Catchen et al., (2011). Population structure was tested at the individual level using STRUCTURE v.2.3 (Pritchard et al., 2000). Ten runs were performed with the admixture model and uncorrelated allele frequencies for *k* values ranging from 2 to 15. Each run consisted of 100,000 MCMC iterations after a burn-in period of 10,000 steps. The most likely value of *k* was determined with the criteria of Evanno et al., (2005) and available in structureHarvester.py (Earl et al., 2012); the final plot was produced after processing the final output in CLUMPP 1.2.1 (Jakobsson et al., 2007) and Distruct 1.1 (Rosenberg, 2004).

Outlier detection and genotype-phenotype-environment associations

SNPs deviating from neutral expectations were detected by scanning the data with two complementary frameworks (Lotterhos & Whitlock 2015). First, SNPs exhibiting atypical values of differentiation (F_{ST}) among OGUs were detected with BayeScan v2.1 (Foll et al.,

2008). We performed twenty pilot runs to adjust parameters, and then conducted a final run consisting of a burn-in of 50,000 chains and 5,000 sampled iterations. Significance was assessed by submitting the log posterior odds ratio to *q*-value and False Discovery Rate (FDR) corrections in R (R Development Core Team, 2013), as recommended in the Bayescan manual (Foll 2012).

Second, given that Bayescan might be inadequate to detect candidate loci along selective gradients or when allele frequencies are correlated within or between localities (De Mita et al., 2013), as could be expected for the Yucatan Jay, Latent Factor Mixed Models (LFMM; Frichot et al., 2013) were used to detect genotype-environment and genotype-phenotype correlations. Analyses consisted of 10,000 iterations that were performed after discarding the initial 5,000 steps as burn-in in the Gibbs Sampling algorithm with 10 repetitions. The number of latent factors was set from one to three and only those loci systematically recovered across analyses with different latent factor values were kept. Significance was assessed in R (R Development Core Team, 2013) by using an FDR threshold of 0.1.

Further associations were explored using the Bayesian method of BayPass V1.01 (Gautier, 2015). The core and the auxiliary variable (AUX) models on BayPass explicitly account for and estimate the covariance structure (Ω) that originates from the shared history of populations, as performed on the Bayenv model (Coop et al., 2010, Günther & Coop, 2013), but exhibiting higher precision and computational efficiency (Gautier 2015). These models have been further shown to be very sensitive for identifying SNPs displaying weak

association signals resulting from soft adaptive sweeps or involved in polygenic characters (Gautier 2015), such as morphological or climate-related variation. Twenty pilot runs of 1,000 iterations each were initially run for adjustment of parameters, and then a final run of 25,000 steps was carried out by taking samples every 250 iterations, after an initial burn-in period of 5,000 steps.

To disentangle stochastic and putatively adaptive processes affecting population structure along the environmental gradient of the Yucatan Peninsula, the relative contribution of environmental (αE) and geographic (αD) distances to genetic differentiation (i.e. allele frequency covariation) was explored with the software BEDASSLE (Bradburd et al., 2013). This was performed for the candidates detected, and, as a control, subsets of markers not retained in the previous analyses. These subsets consisted of putatively neutral marker sets that matched both the number and the MAF of the candidates set. Then for each dataset, the beta-binomial model of BEDASSLE was run for 5 million generations and samples were taken every 100 iterations after discarding the first two million runs as burn-in. Performance and convergence of the models was evaluated by comparing the acceptance rates and parameter trace plots of two replicated runs per dataset according to Bradburd et al., (2013).

Finally, to asses the potential identity of candidate genes putatively involved in adaptive processes, the RAD loci containing the retained SNPs were blasted (MegaBlast) (Zhang et al., 2000) to a multiple genomes available from recent bird genome assemblies (Jarvis et al., 2014). A match was considered positive when at least 80% of sequence identity and an e-value below 1e-4 were obtained. Although limitations exist for pinpointing specific candidate

genes from *de novo*-assemblies or from those constructed based on genomes of other taxa, given that decay of linkage disequilibrium or synteny may vary among species and that scaffolds are not yet arranged into chromosomes, the coding regions located the closest to the regions detected by Megablast were recorded for discussion purposes only. Molecular and biological functions of these genes were obtained from Uniprot, QuickGO, EMBL-EBI databases and from empirical studies on chicken or zebra finch (e.g. Kajimoto et al., 1991; Velho et al., 2005; Hruska et al., 2009).

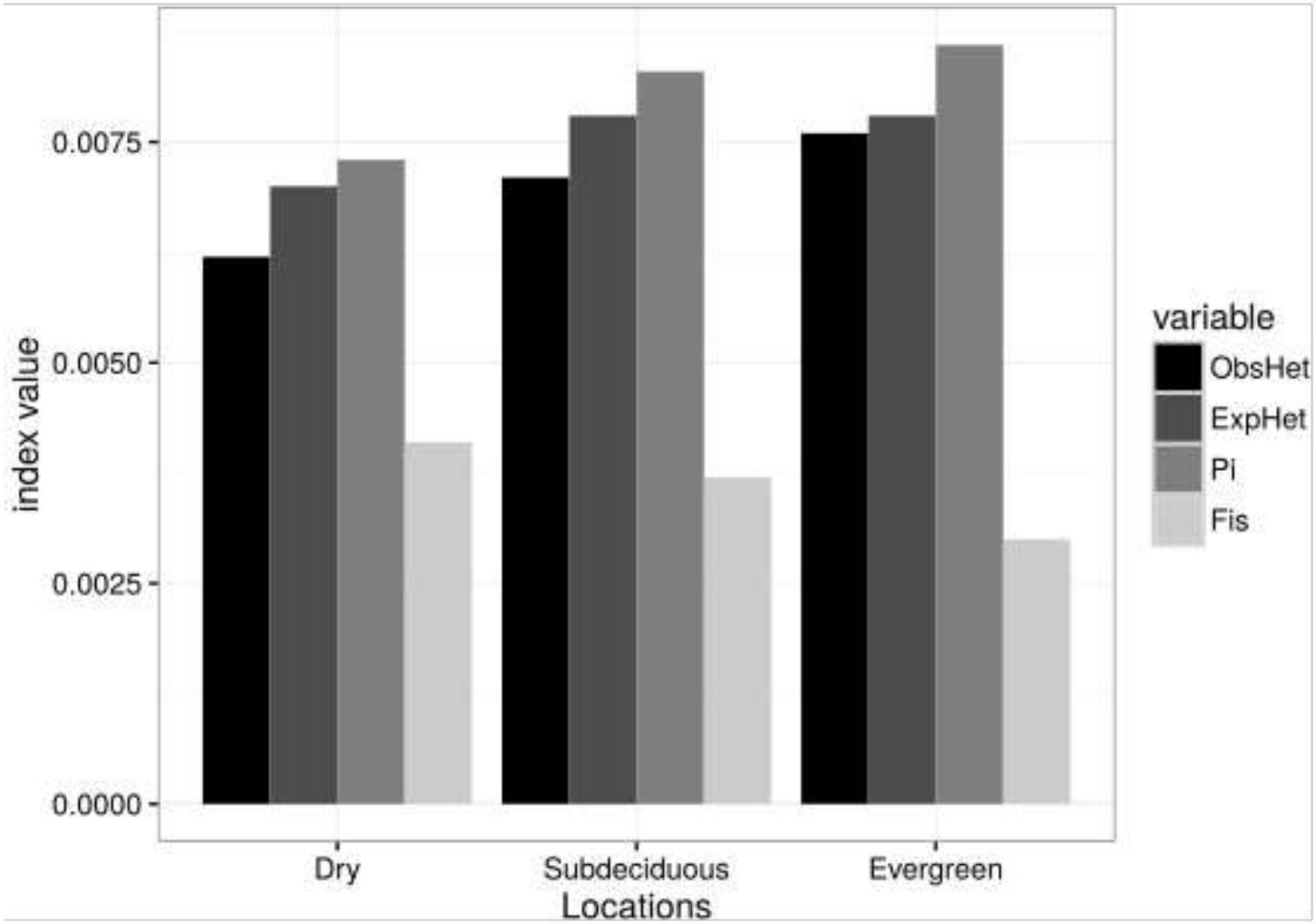
Results

Sequence data and species diversity

In total, 127,869,865 sequencing reads were obtained from 68 individuals. After applying highly conservative filters (see Materials and Methods), the best quality reads were aligned to the American Crow assembly, aligning to ~ 0.02% of its genome. The final dataset consisted of 1,780,314 sequences grouped in 223,031 RAD-tags for 38 individuals. This resulted in 4,040 RAD-loci, 1,649 of which were polymorphic with at least seven individuals per OGU. A mean of 6 SNPs per RAD locus was found, with an average of 13 SNP per *C. brachyrhynchos* scaffold. A positive but non-significant relationship between the number of SNPs and scaffold size was observed ($R^2 = 0.03145$; $P = 0.06382$), thus suggesting an uneven distribution of markers across the reference genome, which is probably the result of low coverage (Figure S7).

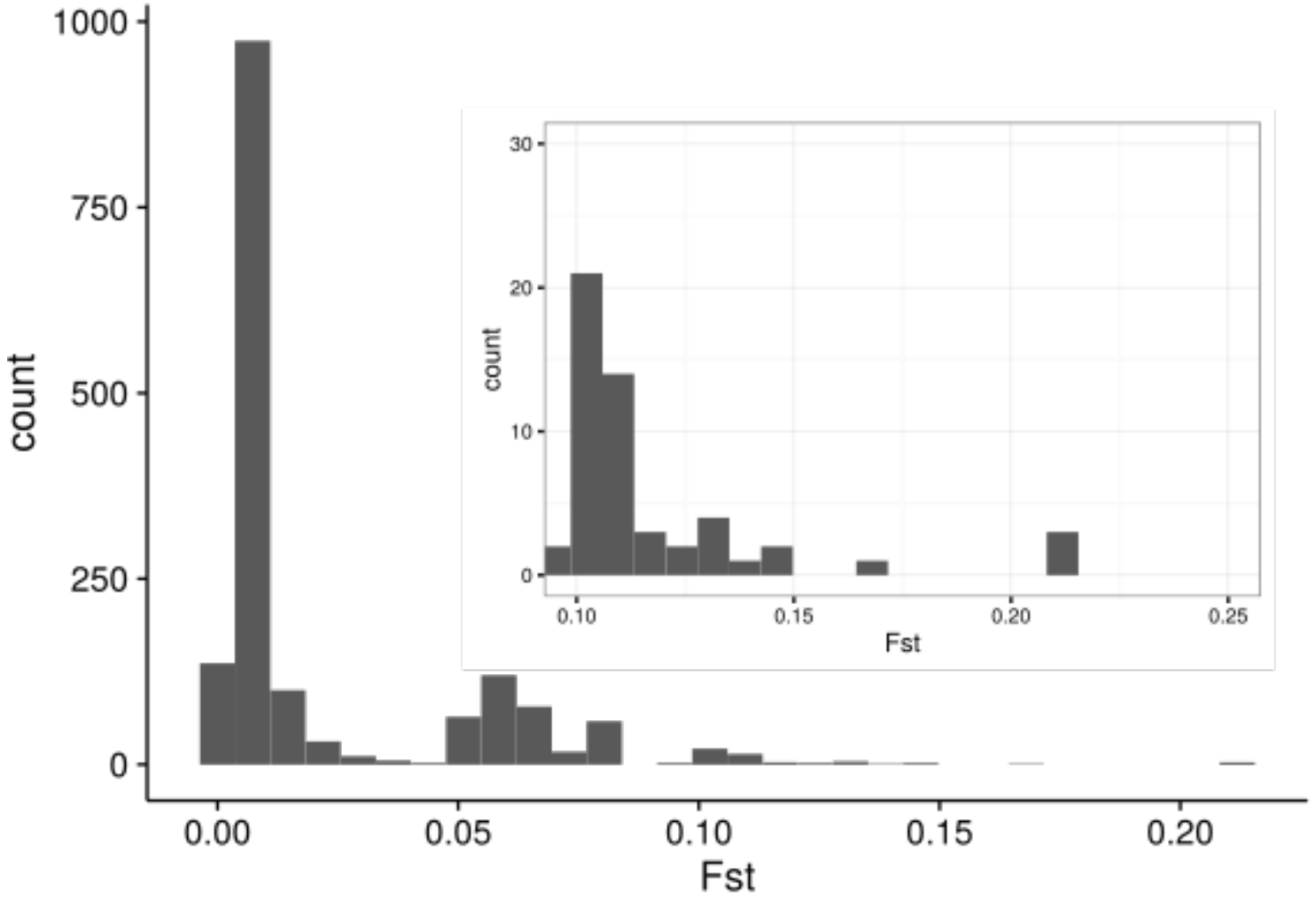
Overall estimates of genetic diversity (H_o, H_e, π and F_{IS}) are summarized in Figure 2. No differences were observed at the species level when all (fixed and variable) or only the variable sites were considered, although variance was larger for the former (Figure S3). Nucleotide diversity among loci ranged between 0.0075 and 0.01 and observed heterozygosity between 0.006 and 0.0076, both values being the highest in the evergreen forest locations. Expected heterozygosities were slightly higher than H_o, although differences were not significant; F_{IS} estimates were positive and ranged between 0.004 and 0.003, were the dry forest had the highest and positive value from the three populations (Figure 2). The genetic differentiation between the three populations with all SNPs are showed in Figure 3. This distribution of the corrected Fst (AMOVA Fst) reveled that the markers with low Fst values are more abundant than those Fst values up to 0. 10., without SNPs with Fst values up to 0.25.

Figure 2: Bar plot of overall estimates of genetic diversity: Observed heterozygosity (ObsHet), Expected heterozygosity (ExpHet), nucleotide diversity (Pi) and endogamy index (Fis), for the three Yucatan jay populations according to three types of tropical forest (dry, subdeciduous and evergreen).



Population structure was low for the Yucatan Jay. The admixture analyses indicated that the most likely number of genetic populations (*k*) was 1, although *k* values of 2 or 3 were also likely, depending on the method used (ln likelihood or delta *k*; See Fig. S13). Despite the lack of marked differentiation among distinct OGUs or forest types, we considered all three values of *k* for the detection of outliers.

Figure 3: Distribution of Fst (the corrected AMOVA Fst) values (histogram) between the three populations calculated for all loci and their high quality SNPs.



Morphological and climatic differentiation

The PCA of morphometric variables showed some differentiation of individuals inhabiting particular forest types, although many birds from the dry forest (TDF; "a" OGU) were often grouped in clusters from other forest types. The first four principle components explained 27.5%, 23.3%, 20 and 13.9% of the variance, respectively. PC1 was mostly loaded by tail length and by bill width, and distinguished individuals from the evergreen (TEF; "g" OGU) and tropical sub-dry forests (TSDF; "d" OGU). The other three PCs only separated some extreme individuals of the TDF from the rest of the sample (Fig. S9). PC2 mostly included variation in wing length and bill depth, PC3 was particularly loaded by culmen, tarsus, and tail lengths, and PC4 was mainly described by tarsus and culmen length variation.

The climatic PCA did not show a clear clustering of individuals, although birds from the TEF were always related to high levels of both temperature and precipitation, while individuals from the tropical dry and sub-dry forest generally exhibited lower values. The first four components explained 35.2, 30.3, 20.7 and 7.8% of the climatic variance, respectively. The main variables loaded into each component are presented in Table S2.

Outlier detection and genotype-phenotype-environment associations

No outlier loci were identified with BayeScan (see Fig S8). However, the associations performed with LFMM and BayPass identified 110 SNPs significantly correlated with either morphological or environmental variables, 12 of which were shared between methods. Three

of these putative candidates were associated with morphological traits, and 9 with environmental parameters (see Table 1 and 2 respectively). Two of the three candidates related to morphology were systematically recovered independently of the value of *k* assumed in LFMM (733 and 6238, see Table S1). The first was a SNP mapped to scaffold 89 of the American Crow genome and to chromosome 2 of Zebra finch. Its closest known gene is an *ARC* (activity-regulated cytoskeleton-associated) gene. It showed significant associations to all morphological PCs except PC3 with LFMM (see p-values histograms Fig S12), and to PC2 and PC4 with BayPass in the Yucatan Jay genome;. The second SNP was mapped to scaffold 146 of the American Crow and to chromosome 2 of Zebra finch, and was correlated with all PCs except PC2 with LFMM and PC1 (p-values histograms Fig S12) and PC3 with BayPass. Its closest known gene encodes a SALL-like protein. The other candidate (4239) was recovered after assuming particular numbers of latent factors (1 and 3, see Table S1) in LFMM and was correlated with PC4 variation with both association methods; its closest gene is a succinyl-CoA ligase.

Among the nine candidate SNPs associated with climate, three were intronic SNPs: SNP 2144 in *CCDC*8 (coiled-coil domain) gene, SNP 7213 in *DAPK* (death-associated protein kinase) gene, and SNP 7557 in *MALDR* (MAM LDL-receptor) gene. Only SNP 2144 was recovered independently of the number of latent factors assumed in LFMM (see Table S1, p-values histograms Fig S11); it was related to PC3 variation (temperature mean of the coldest quarter, seasonality and annual temperature range) with both association methods. The two other SNPs were identified for particular values of *k*, and were associated with all

climatic PCs with both methods. Other than these markers whose RAD-tags blasted to specific genes, three additional SNPs associated with climate are worth highlighting. SNP 4972, located close to an integrin/ubiquitin gene and associated to all PCs with both methods; and 6116, which mapped near a zinc-finger protein gene and correlated with PC3 variation, were recovered with both methods and for all *k* values with LFMM (see Table S1). SNP 12405, located close to insulin-like growth factor and tyrosine-monoxygenase genes, was recovered in both sets of association analyses, climate (PC3) and morphology (PC4) with at least one of the methods used (see Tables 1 and 2).

Table 1: Outlier loci identified in LFMM and BayPass association analyses on phenotype for the four PCs that explained the variance. Candidate genes flanked the sequence after MegaBlasted and molecular/biological function known or hypothesized on birds.

Locus	**Morphometric**								
	PCA-Var* LFMM p-value / BayPass BF				BLAST genes [a]	BLASTed on birds sp. [b]	Scaffold/ Chr [c]	Product	Molecular and Biological function [d]
	PC1	*PC2*	*PC3*	*PC4*					
733 &	5 / NA	5 5 / 3.0		5 / 4.5	LOC104692606 (PSCA)'5 /ARC '3	3	89 / 2	prostate stem cell antigen-like / activity-regulated cytoskeleton-associated	involved in the regulation of cell proliferation. Has a cell-proliferation inhibition activity in vitro /Actin binding, associated with the cell cortex of neuronal soma and dendrites.
12405 &				3.5 / NA	IGF1 5' / LOC104696496 3'	25	56 / 1A	Insulin-like growth factor 1 / tyrosine 3-monooxygenase-like	involved in bone mineralization and maturation / Plays an important role in the physiology of adrenergic neurons
6238 &	NA / 8.9		NA / 9.3	3.5 / NA	SALL 5' / KIAA0319 3'	50	146 / 2	sal-like protein 3 / dyslexia-associated protein	RNA polymerase II core promoter proximal region sequence-specific DNA binding transcription factor activity involved in negative regulation of transcription-pituitary gland development, outer ear morphogenesis gonad development / neuronal migration and negative regulation of dendrite development.
4239 &				4 / 11.4	SUCLA2 5' / HTR2A 3'	3	202 / 1	succinate-CoA ligase, ADP-forming, beta subunit / 5-hydroxytryptamine (serotonin) receptor 2A, G protein-coupled, transcript variant X1	Carbon metabolism / Serotonin receptor activity. Regulation of behavior, hormone secretion.

"&" Loci with SNPS putative under selection also on bioclimatic associations with BayPass higher BF values

* Variables that explain the principal components in morphometry: PC1=TAL+BIW, PC2=WIL+BID, PC3=TAL+TRL+CUL, PC4= TRL+CUL

[a] Features flanking this part of subject sequence on 5' and 3' on the American crow genome

[b] sequence BLASTed on bird species with 80-100% identity and e-value 1e-4 or below. The first two always are American crow and Hooded crow

[c] genes on American crow scaffolds / Zebra Finch chromosomes

[d] molecular and biological function known on Zebra Finch or Chicken, obtained on Uniprot, QuickGO EMBL-EBI.

Table 2: Outlier loci identified in LFMM and BayPass association analyses with environmental variables on the four PCs that explained the variance. Candidate genes flanked the sequence after MegaBlast and with the molecular/biological function known or hypothesized in birds.

LOCUS	Bioclimatic								
	PCA-Var* p value / BayPass BF				BLAST genes[a]	BLASTed on birds sp.[b]	Scaffold/ Chr[c]	Product	Molecular and Biological function[d]
	PC1	*PC2*	*PC3*	*PC4*					
2144 &			4 / 15.18		CCDC85C	7	1 / 5	coiled-coil domain containing 85C	Cerebral cortex development.
29229		NA / 3.6	3 / NA		MCTP1	3	22 / Z	multiple C2 domains, transmembrane 1, transcript factor variant X1	Calcium ion bandin.
4972 &	4.5 / 52.9	NA / 13.0	7.8 / 52.9	NA / 15.4	ITGA4 '5 / UBE2E3 '3	2	255 / 7	integrin, alpha 4 (antigen CD49D, alpha 4 subunit of VLA-4 receptor) / ubiquitin-conjugating enzyme E2 E3	Protein involved in the adherence of cells to other cells or to a matrix / Ubiquitin-like modifier conjugation pathway.
12405		NA / 6.7	4 / NA	NA / 23.8	IGF1 5' / LOC10469 6496 3'	25	56 / 1A	Insulin-like growth factor 1 / tyrosine 3-monooxygenase-like	Involved in bone mineralization and maturation / Plays an important role in the physiology of adrenergic neurons
6116		Na / 4.7	4 / 7.16		ZNF521 '5 / SS18 '3	3	106 / 2	zinc finger protein 521, transcript variant X2 / synovial sarcoma translocation, transcript variant X3	Ligand-dependent nuclear receptor transcription coactivator activity / Metal ion and nucleic acid binding. Neuronal stem cell population maintenance.
17628	NA / 52.9		4 / 21.9		KLHL32 '5 / NDUFAF4 '3	2	14 / 3	kelch-like family member 32, transcript variant X1 / NADH dehydrogenase [ubiquinone] 1 alpha subcomplex assembly factor 4	Mitochondrial respiratory chain complex I assembly / Hormone-regulated proliferation-associated protein of 20 kDa.
7213 &	NA / 16.6	NA / 7	3 / 13.1	NA / 6.9	DAPK1	5	37 / Z	death-associated protein kinase 1	ATP binding and protein kinase activity. Universally important coenzyme and enzyme regulator.
7557&	NA / 14.0	NA / 52.9	3 / NA	NA / 52.9	MALRD1	3	167 / 2	MAM LDL-receptor class A domain-containing protein 1	Cholesterol homeostasis, biosyntetic process.
1041 &	5 / 6	NA / 8.15		NA / 6.4	MPPED2 5' / DNAJC24 3'	14	281 / 5	metallophosphoesterase domain containing 2 / Hsp40 homolog, subfamily C, member 24	Hydrolase activity. Metabolic process / DnaJ-Hsp40 proteins are highly conserved and play crucial roles in protein translation, folding, unfolding, translocation, and degradation.

"&" Loci with SNPS putative under selection also on morphometric associations with BayPass lower BF values

*Variables that explain the principal components in bioclimatic: PC1=Bio15+Bio17, PC2=Bio13+Bio5, PC3=Bio11+Bio4+Bio7, PC4=Bio8+Bio3

[a]Features flanking this part of subject sequence on 5' and 3' on the American crow genome

[b]sequence BLASTed on bird species with 80-100% identity and e-value 1e-4 or below. The first two always are American crow and Hooded crow

[c]genes on American crow scaffolds / Zebra Finch chromosomes

[d]molecular and biological function known on Zebra Finch or Chicken, obtained on Uniprot, QuickGO EMBL-EBI and experimental results from literature.

The twelve candidates further showed significantly higher αE/αD values than random subsets of twelve non-retained SNPs matching the MAF of the candidate set (Table 3). For the candidates, these values were systematically higher than 1.0 across runs (mean = 3.4), whereas for the non-candidate markers, αE/αD estimates were rarely above 1.0 (mean = 0.59), consistent with the idea that other factors other than isolation by distance explain population differentiation of the retained candidates.

Table 3: BEDASSLE simulations results, αE/αD mean ratio and 95% confidence intervals, for outlier and non-outlier SNPs, for each allele and replicate independent runs.

Runs	**Mean ratio αE/αD**	**95% Confidence Interval**
Outlier SNPs		
Allele1	3.48	0.0012 – 7.24
Allele1-rep	1.39	0.0004 – 5.68
Allele2	1.75	0.003 – 3.86
Allele2-rep	6.92	0.002 – 36.07
Non Outlier SNPs		
Allele1	0.49	0.0004 – 1.664
Allele1-rep	0.51	0.0006 – 1.84
Allele2	0.69	0.0003 – 2.23
Allele2-rep	0.69	0.001 – 7.2

The patter of allele frequencies of the retained candidates are showed on Figure 4 illustrating with pie chartz the major and alternative allele frequencies at four SNPs with an IBD patter at the three vegetations types and populations. Also, Figure 5 show the association between the SNPs and the covariables, by a logistic regressions of six SNPs via generalized lineal model significantly predicted by phenotype and bioclimatic variables.

Figure 4: Allele frequencies of major and alternative alleles at four SNPs with an isolation-by-environment patter, represented at three Yucatan Jay populations and vegetation type

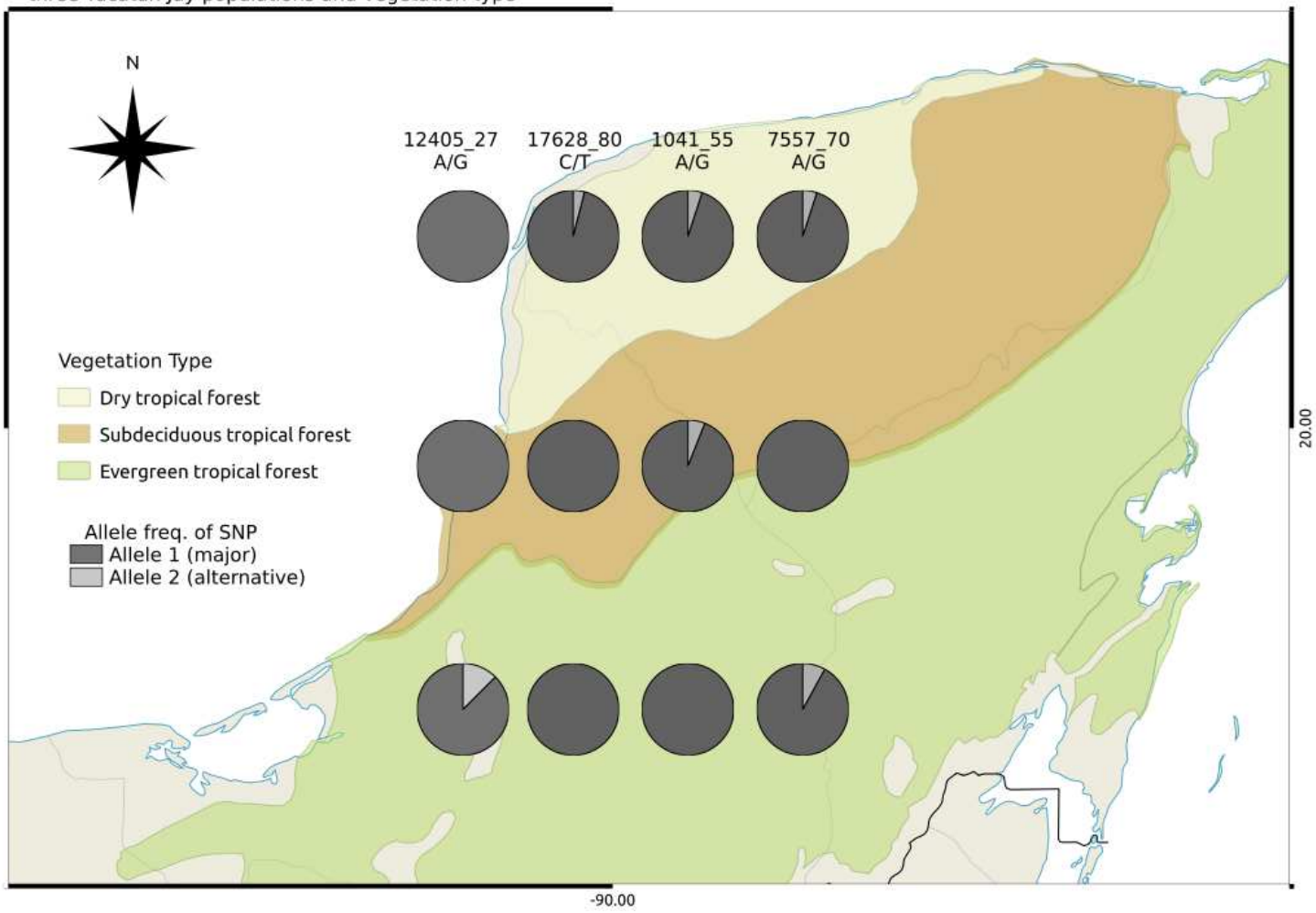
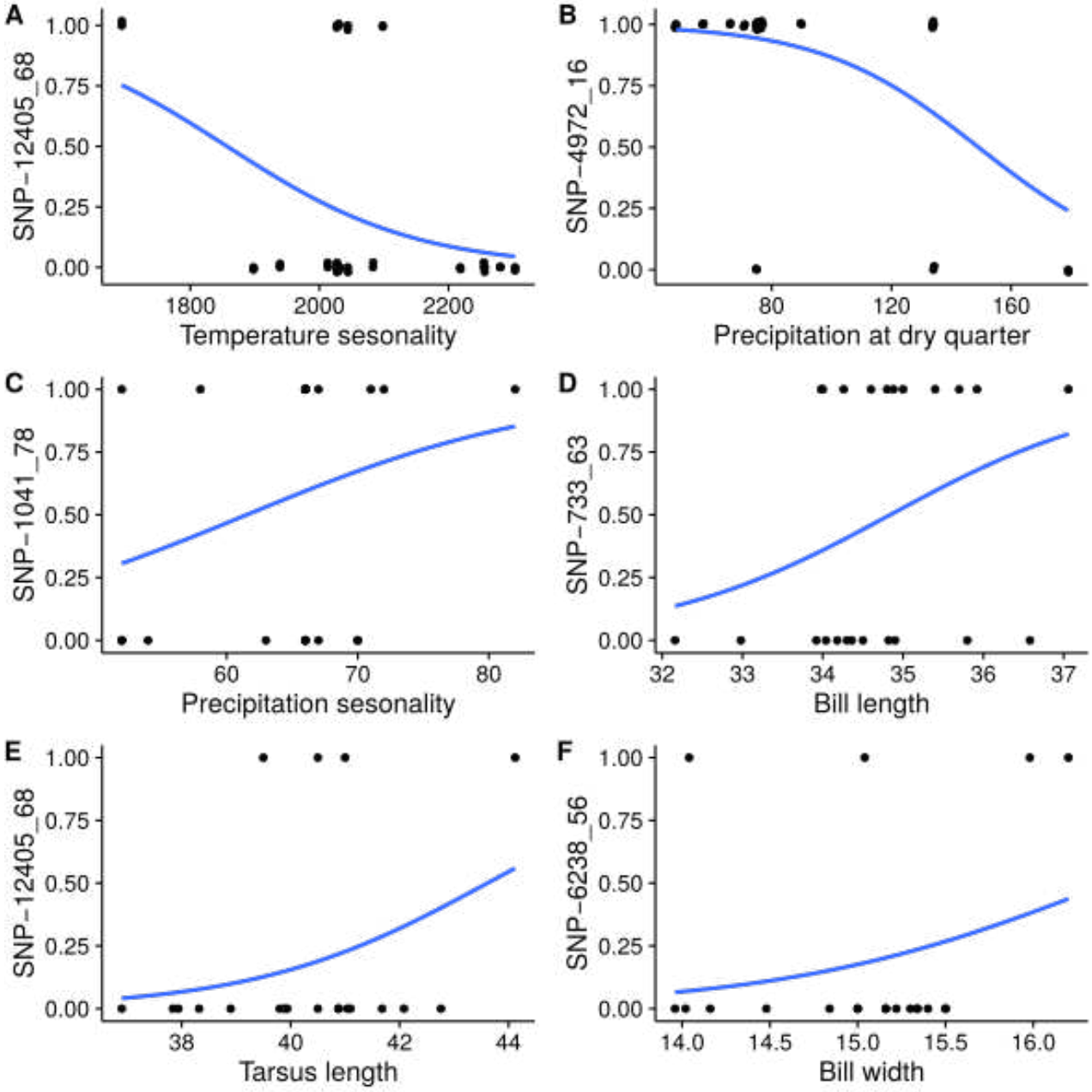


Figure 5: Logistic regression of generalized lineal model of six SNPs/alleles with isolation-by-environment pattern and predicted by phenotype and bioclimatic variables. a)SNP/alleles 12405_68; b)SNP/allele 4972_16; c)SNP/alleles 1041_78; d)SNP/alleles 733_63; e)SNP/alleles 12405_68; f)SNP/alleles 6238_56.



Discussion

This study represents one of the first attempts to use next-generation sequencing technology to identify patterns of genomic variation related to adaptation in an endemic tropical bird. We took advantage of the high synteny recently found across bird genomes (Ellegren, 2013; Zhang et al., 2014; Gossmann et al., 2014; Jarvis et al., 2014) and used the available draft genome of a related corvid (*Corvus brachyrhynchos*), together with stringent bioinformatic to obtain ~1,600 high-quality SNPs for the Yucatan Jay. Employing a battery of complementary analyses, we assessed genome-wide variation and population structure and identified markers related to climate and morphology that conformed to a pattern of isolation by environment. These SNPs could be linked to candidate genes for adaptation, and the genomic regions where they are located represent ideal targets for future genomic surveys in these and other bird taxa.

Despite having a small geographic range and being a cooperative-breeder, the genome-wide nucleotide diversity of the Yucatan Jay (π= 0.009) was relatively high and in the range reported for far more widespread temperate birds like the zebra finch (*Taeniopygia guttata;* 0.01; Balakrishnan & Edwards 2009; Backström et al., 2010) or the willow grouse (*Lagopus lagopus*; 0.008; Quintela et al., 2010) and the White-throated sparrow *(Zonotrichia albicollis*; 0.0076; Huynh et al., 2010). Nucleotide diversity was higher than that for the domestic turkey (*Meleagris gallopavo*; 0.0011; Aslam et al., 2012), great reed warbler (*Acrocephalus arundinaceus;* 0.0012; Backström et al., 2008a) or collared flycatcher (*Ficedula albicollis;* 0.0036 and *Ficedula hypoleuca;* 0.0021; Ellegren et al., 2012). However,

contrary to our expectations, and to previous observations in other cooperative breeders, the diversity of the Yucatan Jay was not spatially structured among locations or vegetation types (k = 1), according to the low genetic differentiation between the three populations (as the Fst distribution showed). Other jays exhibiting similar conjoint reproductive and social structures, like the Western Scrub-Jay (*Aphelocoma californica*) (Mcdonald et al., 1999; Delaney et al., 2008) or the Apostlebird (*Struthidea cinerea)* (Woxvold et al., 2006) have indeed exhibited significant genetic differentiation, especially among breeding flocks distributed in small geographic areas. Our findings may suggest that the characteristic seasonal fusion-fission dynamics of the Yucatan Jay (Raitt et al., 1976) promptes gene flow through inter-flock migration. However, given that our sampling design was not designed to capture fine-scale genetic structure, this possibility remains a hypothesis for the future.

Another factor that may explain the lack of population structure in the Yucatan Jay is its continuous distribution across a peninsula mostly covered by forests and that has no obvious geographic barriers to gene flow (i.e. there are no mountain ranges and all rivers are subterranean). Such a distribution is more consistent with a gradient variation of allele frequencies such as isolation by distance and/or environment, as suggested by results (see Table 4), than with an island model to identify genetic clusters. Moreover, despite lacking quantitative measures of dispersal, Yucatan Jay flocks appear highly vagile and are able to cover 1 or 2km in less than a hour, especially once the breeding season has finished (Raitt & Hardy 1976; FTG personal observations). Such high vagility should conform better to an isolation by distance/environment framework than to an island model, and could also account

for the lack of population structure in Yucatan Jay.

Previous simulation works have shown that methods relying on genotype-environment (phenotype) associations (GEA) are the most adequate for identifying polymorphisms related to adaptation under isolation by distance/environment scenarios, while outlier-based algorithms generally perform poorly in most of these frameworks (e.g. de Mita et al., 2013; Lotheros & Whitlock 2014; Villemereuil et al., 2014). In this study we detected 13 and 97 loci putatively associated with climate and morphology with LFMM and BayPass, respectively. While we acknowledge that some of these loci could represent false positives, it must be noted that our sampling design (a few individuals per flock across many locations per OGU encompassing most of the species range) allowed for a good performance of the GEA methods (i.e. by diminishing relatedness and allele frequency autocorrelation), thus making it unlikely that all correlations found herein are spurious (see de Mita et al., 2013 for a more detailed discussion).

The BEDASSLE analyses further showed that the spatial distribution of alleles at the 12 retained candidates was more affected by environmental variation than by geographic distance (i.e. isolation by environment), while the opposite was true for the non-retained markers (i.e. isolation by distance). Such patterns can be produced by either reduced dispersal across habitats, by strong local selection forces or a combination of both. Given the absence of obvious barriers to gene flow in the Yucatan Peninsula and the lack of overall genetic differentiation across OGU, we hypothesize that environmental conditions across forest types might exert differential pressures at specific targets throughout the Yucatan Jay's

genome. In such case, morphological PC4 (culmen) and climate PC3 (lowest temperature), which were the most prevalent variables among correlations across all analyses, may suggest clues to the underlying mechanisms driving isolation by adaptation in this species.

The Yucatan Jay has been described as an omnivorous, opportunistic bird that capitalizes on temporary and localized food sources as varied as caterpillars, berries or slugs (Raitt & Hardy 1976). However, food supply differs greatly across years and local habitats in the Yucatan. For instance, in seasonal forests like the TDF, fruit availability is usually restricted to the rainy season, while some invertebrates might be accessible throughout the year. By contrast, in the less seasonal TEF, both fruits and invertebrates can easily be obtained throughout the year (Arita & Rodríguez 2002; Ramírez-Barahona et al., 2009; Vázquez-Domínguez & Arita 2010; Islebe et al., 2015). Such differences might translate in contrasting dietary pressures between forest types, and thus be reflected at the morphological level, particularly in bill shape and size. Bills are among the most plastic morphological structures in birds, and bill variation has provided some classic examples of local adaptation for over a century (e.g. Darwin, 1845; Baldassarre et al., 2013; Luther & Greenberg 2014).

Thus a short list of four candidate genomic regions for bill shape variation suggests some promising avenues for future studies, especially if the markers detected here are linked to the actual targets of selection. Although such linkage remains to be confirmed, the genes revealed by blast searches were located relatively far away from the matching regions, between 56Kb and 108Kb, in the zebra finch genome. However, as the recombinational landscape of the Yucatan Jay is unknown, it is still far too early to completely discard these

genes. For example, all the loci containing the candidate SNPs for bill variation were aligned to regions of chromosomes characterized by low recombination in the zebra finch (i.e. 1, 1A, and 2; Backström et al., 2010), implying that, should a similar recombinational landscape be present in the Yucatan Jay, LD could be maintained over long distances and these genes, or noncoding regions regulating them, might thus represent real candidates for future studies (Edwards et al., 2015).

The genes near the candidate genomic regions associated to bill shape are (enlisted below) required for development on vertebrates and mutations in these genes are associated with diseases, they respectively coded for: an activity-regulated-cytoskeleton-associated *(ARC*) gene, an Immediate-Early Gene (IEG) down-regulated by birdsong stimulus (Farivar et al., 2004) because transcript level can be altered by auditory imprinting (Bock et al., 2005). Also, contribute to synaptic plasticity, memory (Velho et al., 2005) and spatial learning (Leitner et al., 2005); Other gene is the prostate stem cell antigen-like (*PSCA*), a modulator of signaling-induce the cells to die (e.g. during development of parasympathetic nervous system, Hruska et al., 2009), genetic variations in this gene cause diseases (e.g. diffuse-type gastric cancer, Sakamoto et al., 2008); the insuline-like growth factor I *(IGFI*) gene highly conserved during recent vertebrate evolution, regulates aspects of growth, development and differentiation (Kajimoto et al., 1989; Kajimoto et al., 1991), specially in bone mineralization and maturation (Ballard et al., 1990; Fisher et al., 2005). Has been identified as a candidate for growth in chicken populations (Gheyas et al., 2015), in the Atlantic herring associated to a salinity gradient (*Clupea harengus,* Günther et al., 2013) and in human populations (Frichot et

al., 2013); the tyrosine 3-monooxygenase-like (LOC104696496) gene that encodes for an enzyme responsible for catalyzing a precursor for dopamine (L-DOPA) and the synthesis of catecholamines (Nagatsu et al., 1995) which in rodents affect the social rank during the process of gene expression (Pohorecky et al., 2004) and in teleost (*Oryzias latipes*) influence the sexual dimorphism (Kawabata, et al., 2012); the *SALL-like* protein (*SALL*) gene important in limb development (Akiyama et al., 2015) and regulates transcription in embryonic stem cells (Milanovich et al.,2015); the dyslexia-associated protein (KIAA0319) gene that (with other genes TTRAP/THEM2) plays an important role in human language development (Pinel et al., 2012) and phoneme processing in auditory cortex (Centanni et al., 2014), mutations in this gene are associated with dyslexia (Cope et al., 2005); the Succinyl-CoA ligase (SUCLA2) gene encodes for a mitochondrial matrix enzyme (Johnson et al., 1998; Miller et al., 2011; Dobolyi et al., 2015), mutations in this gene are associated with severe muscular atrophy (mitochondrial DNA depletion syndrome, Ostergaard et al., 2009); the 5-hydroxytryptamine (serotonin) receptor 2A (HTR2A) gene that encodes one of the receptors for serotonin, an other neurotransmitter (Seamans & Yang 2004), mutations in this gene are associated with neuropsychiatric diseases (like schizophrenia and obsessive-traits, Banlaki et al., 2015, Juárez et al., 2013)

Low temperatures, on the other hand, are important limiting factors for the distribution of tropical birds. Even if corvids are a mostly temperate family, the restrictions that impose temperatures below the physiological limits of a species should be strong enough to generate adaptive patterns across a genome. Three of the candidate SNPs associated with climate

were located in RAD-loci matching introns of known coding genes. These genes are: the coiled-coil domain containing 85C (*CCDC*8) gene, important for the proliferation of epithelia in organs (in rats, Tanaka et al., 2015) and for the cortical development (Mori et al., 2012); the death-associated protein kinase 1 (*DAPK*) gene a tumor suppressor (e.g. promote hypermethylation, Kawaguchi et al., 2004) that protect neurons from hypoxic-ischemic injury (Schumacher et al., 2002; Shamloo et al., 2005) and two SNPs are associated with disease (e.g. late-onset Alzheimer's, Li et al., 2006); the MAM LDL-receptor (*MALDR*) gene involve in regulating bile acid biosynthetic process in cholesterol homeostasis (Mouzeyan et al., 2000; Phan et al., 2002; Vergnes et al., 2013); finally the multiple C2 domains, transmembrane 1 (MCTP1) gene involve in regulating synapses and recycling of Central Nervus System neurons (mutations cause neuropsychiatric diseases, Qiu et al., 2015). All these genes due the importance of the coding region constitute candidates for future studies.

Other SNPs with high values of association in temperature (seasonality, cold and mean temperature) and precipitation (seasonality and in driest quarter) in both methods, are interesting to mention because the target of selection are near genes involved in aspects of physiology and metabolic efficiency also. These genes are the ubiquitin-conjugating enzyme E2 E3 (UBE2E3) gene that is essential for the proliferation and differentiation of retinal cells (Debonneville & Staub 2004; Plafker et al.,2008); the integrin, alpha 4 (ITGA4) gene involved in production of immunoglobulins and increased expression in birds susceptible to the colonization of bacteria (Connell et al., 2012); the kelch-like family member 32 gene (KLHL32) associated with body mass index in human populations with evidence of recent

positive selection in and downstream (Monda et al., 2013); and the NADH Dehydrogenase (Ubiquinone) Complex I, Assembly Factor 4 (NDUFAF4) gene that encodes a complex I in mitocondrial assembly (Saada et al., 2008) and mutations in this gene are a cause of severe mitochondrial complex I deficiency and its critical for the regulation of oxidative stress (Schlehe et al., 2013)

Some SNPs with low values of association with bioclimatic variables (e.g. temperature warmest month) are interesting to mention because were recovered in two latent factors and with both methods, and were near: the zinc finger protein 521 (ZNF521) gene that with other gene (Runx2) regulates osteoblast differentiation and maturation of bones (Hesse et al., 2010; Spina et al., 2013); the synovial sarcoma translocation (SS18) gene essential for early embryonic development through the regulation of cell migration (Kimura et al.,2009) and is ubiquitously expressed in early embryogenesis (in mice, de Bruijn et al.,1996); the metallophosphoesterase domain containing 2 (MPPED) gene responsible for metabolic process as hydrolase activity; and the Hsp40 homolog, subfamily C (DNAJC) gene related to the pineal gland molecular mechanisms (conserved domain) that underly time-of-day-dependent responses to light (e.g. as chaperon of Hsp70s gene-protein, Hatori et al., 2011; Ahmad et al., 2011).

Additional SNPs exhibiting associations with morphology were detected in BayPass, although at lower levels of significance. The most prominent among these was SNP 12405, whose RAD-locus matches, in the zebra finch, a part of the long intergenic region between the above mentioned *IGF1* gene and a tyrosine 3-monoxygenase gene, which corresponds

fairly well with the association with temperature detected herein.

The identification of candidate SNPs simultaneously related to climate and morphology might well be reflecting the association between forest types, food availability and morphological variation previously described for the Yucatan Jay (Chablé-Santos 1999). However, it may also suggest that joint selective forces acting between habitats are affecting many targets both coding and noncoding, across the genome, producing complex pattens of differentiation likely driven by many genes. Such polygenic selection generally results in minor allele frequency changes, each one explaining but a part of the total phenotypic variance of a species (Vaysse et al., ., 2011; Korte & Farlow 2013; Fariello et al.,2014). In all likelihood we have detected only a fraction of the genes implicated in such differentiation in the Yucatan Jay. Finally, this work also achieve the presence of the isolation-by-environmental pattern an footprints of selection in presence of high gene flow. Despite the controversial about these issues, recently have been reported that Isolation by environment its also (as isolation by distance pattern) common in nature (Mendez et al., 2010; Mallet et al., 2014; Dennenmoser et al., 2014; Manthey & Moyle 2015; Lonsinger et al., 2015) and the strength of selection can be detected in presence of high gene flow (Nielsen et al., 2009; Saint-Laurent et al., 2003; Schweizer et al., 2016) where environmental conditions affect synchronization of mating and patterns of dispersal (Sexton et al., 2014), as probably happened in the Yucatan Jay where the dynamics of the cooperative breeding social system can be altered by the environmental gradient. Additional genomic work in this and other tropical species can further inform patterns of diversification in neotropical birds.

DISCUSIÓN Y CONCLUSIONES GENERALES

Los resultados de esta tesis sugieren que la chara yucateca presenta adaptación respecto al gradiente ambiental de su área de repartición, inclusive en presencia de alto flujo génico entre poblaciones. Esta adaptación se ve reflejada en la variación intraespecifica de la organizacion social, en la variación morfométrica y en la variación genética. Estas tres características mostraron asociación con las restricciones del gradiente ambiental de la península. Es posible que ocurra variación más profunda en el sistema social en la chara, por lo que valdría la pena explorarlo con estudios a largo plazo. La variación en regiones genómicas candidatas a selección que mostraron un patrón de aislamiento por el ambiente y que además estuvieron asociadas a la morfometria, pueden ser importantes blancos para futuros estudios en esta especie y otros taxa de vertebrados, pues estas regiones están asociadas con mecanismos adaptativos que van desde el desarrollo de los sistema nervioso y oseo, hasta el metabolismo, la conducta social y la inmunidad. Considerando que la chara yucateca no tiene ninguna barrera geográfica aparente que limite su movilidad, esta tesis demuestra que la hipótesis más factible es la presencia de aislamiento por ambiente y adaptación local entre las poblaciones más contrastantes del gradiente.

Es muy probable que la chara yucateca ajuste su sistema social de acuerdo con las restricciones ambientales y temporales, como fue detectado en el capítulo II de esta tesis. Los tipos de vegetación, la temperatura y la constancia en la precipitación son variables ambientales que se relacionaron con el número de individuos, particularmente de subadultos,

que componen los grupos sociales. El patrón diferencial entre los tipos de vegetación en las fases de la estación reproductiva (mencionadas por Raitt y Hardy 1976), sugiere que otras estrategias sociales como las dinámicas de fusión-fisión, también son ajustadas a las restricciones ambientales, formando parte de las estrategias ecológicas en esta especie. Esta estrategia ya fue detectadas en otras aves con crianza cooperativa (Griesser et al., 2009) y valdría la pena analizarla con estudios a largo plazo en la chara yucateca en todo el gradiente ambiental.

La organización social, a pesar de ser una variable muy plástica, refleja la dinámica de las estrategias sociales que pueden tener implicaciones adaptativas, como es el retraso en la dispersión (Emlen 1995, Russell 2004, Koenig y Dickinson, 2004; Baglione et al., 2006; Canestrari et al., 2012). En otras especies de charas se puede observar variación en el tamaño de grupo entre subespecies como *C. samblasianus y C. samblasianus nelsoni* (Raitt y Hardy 1976; Peterson 1991), y en otros casos como en *Aphelocoma ultramarina,* donde ya se ha argumentado que esta variación puede estar relacionada con la historia evolutiva (Brown y Horvath 1989; Peterson 1991). Los córvidos han demostrado ajustar su organización social de acuerdo a la disponibilidad de los recursos (Baglione et al., 2006, Canestrari et al., 2012), a tener tasas de especiación rápidas (Edward y Naeem 1993; Feduccia 2003; Bonaccorso et al., 2010), a ser grandes explotadores ecológicos y a tener una distribución global (Blake y Vaurie 1962; Goodwin 1976; Madge y Burn 1994; Ekman y Ericson 2006). Bajo esta perspectiva, encontrar un ajuste en la organización social respecto al ambiente resulta un planteamiento factible para la chara yucateca. Por lo tanto, esta tesis

sugiere que la variación en la organización social es parte de un complejo de estrategias sociales para adaptarse a los tipos de vegetación (dieta) y al clima de la península.

Si se prosigue con este planteamiento, donde la chara yucateca ajusta sus estrategias sociales a las restricciones del gradiente ambiental, el capítulo III podría ofrecer sustento a este resultado, a pesar de desarrollarse en escalas temporales distintas. Es importante mencionar que el estudio genético se elaboró con muestras de hace 20 años, haciendo el mejor uso posible de las colecciones nacionales de México que permiten desarrollar estudios poblacionales. Por ello, se considera que los dos último capítulos de esta tesis, tan solo nos aproximan a entender de manera independiente los patrones ecológicos y procesos adaptativos en esta especie, con reserva en la conexión entre ambos. Aún así, abren nuevos planteamientos e hipótesis para poner a prueba y desarrollar en esta especie y en esta región de México. Cabe mencionar que ambas resultan excelentes modelos de estudio sobre la evolución biológica de las aves neotropicales y sus conductas sociales.

A través de análisis de asociación a nivel genómico de los genotipos con el ambiente y el fenotipo, se detectó adaptación local en la chara siguiendo el gradiente ambiental de la Península de Yucatán. Los sitios candidatos a selección natural detectados en el genoma de la chara yucateca se encuentran cerca de o en genes codificantes (regiones intergénicas e intrones), lo que implicaría efecto genético de "*hitchhiking*" (Maynard-Smith et al., 1974; Stephan, 2010; Shikano et al., 2010). Los SNPs candidatos identificados simultáneamente con clima y morfología reflejan la asociación con el tipo de vegetación, la disponibilidad de recursos y la variación morfológica descrita previamente (Chablé-Santos 1999).Estos

incluyen genes como el *IGF1* (Insulin-grow factor 1) que influye en el desarrollo y maduración de la estructura ósea (Kajimoto y Rotwein 1989; Kajimoto y Rotwein 1991). También sobresalen el gen SALL encargado del desarrollo de las extremidades (Akiyama et al., 2015), el gen *KIAA0319* importante en el desarrollo del lenguaje (estudiado en humanos, Pinel et al., 2012) y el proceso de fonema en el cortex auditivo (Centanni et al., 2014), el gen *SUCLA2* que codifica una enzima de la matriz mitocondrial (Johnson et al., 1998; Miller et al., 2011; Dobolyi et al., 2015), el gen *HTR2A* que codifica para un de los receptores de serotonina y otros neurotransmisores (Seamans y Yang 2004) y el gen *ARC* (activity-regulated cytoskeleton-associated), de expresión inmediata temprana (IEGs por sus siglas en inglés, *"Immediate early gene"*) regulado por el estímulo del canto en las aves (Farivar et al., 2004; Bock et al., 2005). Este último contribuye en la plasticidad sináptica, la memoria (Velho et al., 2005), el aprendizaje espacial (Leitner et al., 2005) y está implicado en respuestas conductuales como la impronta filial (Bock et al., 2005), la cual en aves afecta las relaciones socio-emocionales entre hermanos y padres (Bolhuis 1991). Todos estos genes han sido ubicado en el mismo cromosoma (el 2) en *Taeniopygia guttata* y *Gallus gallus*, ver tabla 1 y tabla 2 del capítulo III), el cual se ha reportado que contiene bloques de genes relacionados con conductas sociales y presenta baja recombinación (Thomas et al., 2008; Gossmann et al., 2014). Puede ser factible que los genes de esta región genómica se encuentren bajo las mismas fuerzas de selección y por lo tanto asociados al desarrollo de la misma estrategia social, la crianza cooperativa, en la chara yucateca. Sin embargo esta hipótesis aun debe ser probada.

Bajo la perspectiva del extenso trabajo experimental en el gen *ARC* y las conductas sociales en algunos vertebrados (mencionadas arriba), cabe reflexionar que la impronta en aves podría ser afectada por la variación en la organización social (tamaño de los grupos y composición de edades). El patrón de relación de la organización social y la composición social con el ambiente, en el capítulo II, incita a pensar que este gen podría ser transcrito diferencialmente entre las poblaciones del gradiente ambiental, donde se estarían desarrollando diferentes niveles de impronta filial en los neonatos. De esta forma donde ocurre mayor retraso en la dispersión de las primeras generaciones, se permitiría el reconocimiento con la vocalización de todos los integrantes de la unidad social. Como fue mencionado en la conclusión del capítulo I, de esta manera la crianza cooperativa podría ser favorecida en cohesión y reconocimiento de co-específicos para que ocurra la cooperación. Un desarrollo experimental sobre los niveles de expresión del gen *ARC*, el tamaño de los grupos sociales y la frecuencia de conductas de cooperacion podrían dar un aproximado a la prueba de esta hipótesis.

Las bases genéticas de la cooperación pueden ir más allá de una relación genética y pueden ser señales de reconocimiento no visibles al ojo humano (Mateo 2004, Moore 2007, Leclaire et al., 2013; ver también caítulo I) con posibles efectos pleiotrópicos, epigenéticos o epítasis. Esta tesis no pretende probar las posibles bases genéticas de la crianza cooperativa con/en la chara yucateca. Pero ha aportado una lista de regiones candidatas a selección natural en un córvido neotropical que emplea estrategias sociales como la crianza cooperativa y que habita un gradiente ambiental donde presenta adaptación local. Por lo

tanto, sería de gran interés comprobar los niveles de expresión de estos genes experimentalmente con un enfoque "*Top-down*" (Rellstab et al., 2015). Para tal estudio tal vez sea necesario emplear cruzas controladas de individuos de poblaciones con condiciones contrastantes y el seguimiento de las generaciones (para controlar desequilibrio de ligamiento), y así encontrar los genes asociados a la estrategia y el sitio exacto que se encuentra bajo selección. Para tal fin sería necesaria la re-secuenciación de la región que contiene el gen o de transcriptomas para, implementar estudios de asociación genómica a escala fina (GWAS) con mapeo de QTLs *"quantitative trait locus"* y mapas de desequilibrio de ligamiento (para lo cual es necesario secuenciar el genoma de referencia específico). Sin embargo, todavía para especies *no modelo* el enfoque "*Top-down*" representa un reto, sobre todo en poblaciones naturales (Rellstab et al., 2015). Para tal caso, un enfoque *"Bottom-up"* como el que fue realizado en el capítulo III, pero haciendo comparaciones entre especies o géneros (genética de poblaciones comparada) que habiten gradientes ambientales y que expresen crianza cooperativa, podrían mostrarnos regiones semejantes candidatas a selección. Estas especies podrían ser *Lamprotornis superbus* en Africa o *Pomatostomus temporalis* en Australia.

En este punto cabe resaltar la importancia de las regiones intergénicas como detectores de genes candidatos por efecto *hitchhiking* en especies *no modelo* (Gagnaire et al., 2015). Este efecto genético ha demostrado ser poderoso para detectar regiones genómicas candidatas a selección (Schlötterer, 2003; Hohenlohe et al., 2010; Oleksyk et al., 2010; Whiteley et al., 2011), lo cual resulta un paso práctico para la genómica funcional en

genética de poblaciones (Schlötterer, 2003) y muy útil en poblaciones naturales. Sin embargo, las fuerzas selectivas que están actuando entre hábitats en la chara yucateca podrían estar afectando muchos blancos en todo el genoma, produciendo un patrón complejo de diferenciación. Por lo tanto en el presente trabajo se ha detectado solo una fracción de los genes implicados en la diferenciación en la chara yucateca, probablemente debido al protocolo empleado con el que se obtuvo baja cobertura genómica. Cabe notar que debidoa este protocolo, el poder estadístico y el diseño experimental pueden tener consecuencias para detectar adaptación local (Lotterhos y Whitlock 2015). El protocolo ddRAD-seq permite seleccionar regiones genomicas al azar conforme a las enzimas de restricción empleadas durante la elaboración de la bibliotecas genómicas (Peterson et al., 2012). Por ello, muchas regiones que son eliminadas durante este proceso quedan fuera del analisis con la posibilidad de que estas regiones, que no estan pudiendo ser vistas, también esten bajo selección.

El patrón de aislamiento por ambiente detectado en los sitios candidatas a selección, fue encontrado a pesar de la presencia de alto flujo génico entre las poblaciones de la chara. Escenario que causa controversia, ya que la presencia de alto flujo génico podría impedir la fijación de adaptaciones locales (discutido por varios autores desde Haldane 1930, Wright 1943 hasta Bridle et al., 2010), por lo que el asilamiento por distancia es un patrón que ha resultado más común en la naturaleza (Slatkin 1993; Meirmans 2012; Wang et al., 2013). Sin embargo, actualmente, el patrón de aislamiento por ambiente ha explicado las diferencias genéticas en varios taxa en plantas y animales (Saint Laurent et al., 2003, Nielsen et al.,

2009, Mendez et al., 2010, Mallet et al., 2014, Dennenmoser et al., 2014, Manthey y Moyle 2015, Lonsinger et al., 2015, Schweizer et al., 2016). Estos nuevos hallazgos prometen nuevos planteamientos teóricos en genética de poblaciones, respecto a las fuerzas selectivas operantes y las dimensiones a considerar (discutido en el capítulo I). Sobre todo, lleva a cuestionar la interacción entre dichas fuerzas evolutivas en poblaciones que desarrollan sistemas sociales u estrategias sociales como la cooperación, que podrían involucrar varias escalas de selección, así como una fuerte selección social y selección sexual en ambos sexos. Esto se ha detectado recientemente en especies de aves que desarrollan crianza cooperativa, donde se hace especial hincapié en considerar la implicación que tiene el que ambos sexos estén bajo las mismas presiones evolutivas para tener acceso a la pareja reproductiva (Apakupkul y Rubenstein 2015). Finalmente, esto demuestra que estamos en el proceso de reelaboración en genética de poblaciones, sobre la teoría de las dimensiones y fuerzas selectivas operantes en poblaciones con estrategias sociales cooperativas o altruistas.

Contrario a lo esperado, no se encontraron las implicaciones que en principio se esperaban de la crianza cooperativa en la estructura genética de las poblaciones de la chara yucateca, tales como una alta diferenciación y/o altos niveles de endogamia (Lott 1991; Beck et al, 2008; Berg et al, 2009). Esto fue debido a la escala de análisis que se decidió desarrollar para tener la resolución de los análisis de asociación. Dichos análisis no son compatibles con un estudio sobre la estructura familiar. Es importante resaltar que el muestreo geográfico de la presente investigación no fue a fina escala como en otros trabajos

(Mcdonald et al., 1999; Woxvold et al, 2006; Delaney et al., 2008). La selección de los genotipos para los análisis de asociación requirió que fueran individuos con relación menor a la de tercer y cuarto grado (ver capitulo III), es decir con el menor valor de parentesco posible. Para un análisis detallado de la estructura genética a una escala más fina, es necesario tener control parental de los individuos y su identidad (tener marcados a los individuos) para hacer análisis de paternidad y obtener la relación genética a escala fina (a nivel de grupo social), lo cual sería importante hacer comparativamente en los tipos de vegetación contrastantes para futuros estudios.

Como conclusión final de esta tesis, cabe enfatizar que se utilizó la complejidad de las poblaciones naturales de la chara yucateca, para estudiar los patrones, procesos y posibles mecanismos involucrados en la evolución y adaptación al gradiente ambiental que habita. Gracias a la distribución de esta especie fue posible reconocer su naturaleza adaptativa y las causas ambientales o ecológicas, como ya se han obtenido en otros estudios recientes en varios taxa con métodos genómicos similares (Günther y Coop 2013; Dennenmoser et al., 2014; Manthey y Moyle 2015; Schweizer et al., 2016). Es decir, la crianza cooperativa podría ser una estrategia adaptativa, evolutivamente estable reforzada con bases genéticas en la chara yucateca. Sin embargo, cabe reflexionar que las señales de reconocimiento de con-específicos pueden estar coordinadas por bases genéticas, no como una determinante de la conducta, sino como un conjunto de efectos y causas multidireccionales entre el genotipo y el ambiente, que resultan en un fenotipo determinado (el gen *ARC* puede ser un buen ejemplo de éste proceso). Conocer los mecanismos biológicos del proceso adaptativo en poblaciones

naturales es un campo de investigación en desarrollo. Este campo de investigación está ayudando a comprender el papel y el potencial de la conducta en la evolución y en los cambios genéticos en vertebrados (Lamichhaney et al., 2016; Schweizer et al., 2016).

Es probable que estrategias sociales como la crianza cooperativa, así como el altruismo, que durante décadas han sido un tema controversial dentro de la biología evolutiva y la ecología, puedan ser abordadas desde una renovada perspectiva con los nuevos métodos genómicos y la expansión del marco teórico de la biología evolutiva (EES). En el capítulo I se menciona que el efecto pleiotrópico puede estar relacionado con el desarrollo de la conducta de cooperación. Sin embargo, la posibilidad de que la cooperación sea una estrategia evolutiva regulada por múltiples genes resulta una hipótesis altamente factible, como lo ha demostrado el estudio de Lamichhaney et al., (2016) en *Philomachus pugnax* donde bloques de genes contenidos en una inversión cromosómica son los responsables de los morfotipos que permiten el desarrollo de la conducta reproductiva tipo "lekking" o "arenas". No obstante, cabe enfatizar para el futuro desarrollo en este campo, que la existencia de bases genéticas que explican la expresión de conducas sociales, no pueden ser vistas como la causa determinante, pero sí como el efecto epigenético de la conducta y el ambiente social.

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Apéndices Capítulo II

Figure 1. Principal Component Analysis (PCA) plot with 18 WorldClim bioclimatic variables of the Yucatan peninsula at each point were a Yucatan Jay social group were found. PCs that represent more than the 94% of the variance. Groups represented the three predominant vegetations types: TDF=Dry tropical forest, TSDF=Subdeciduous tropical forest and TEF=Evergreen tropical forest.

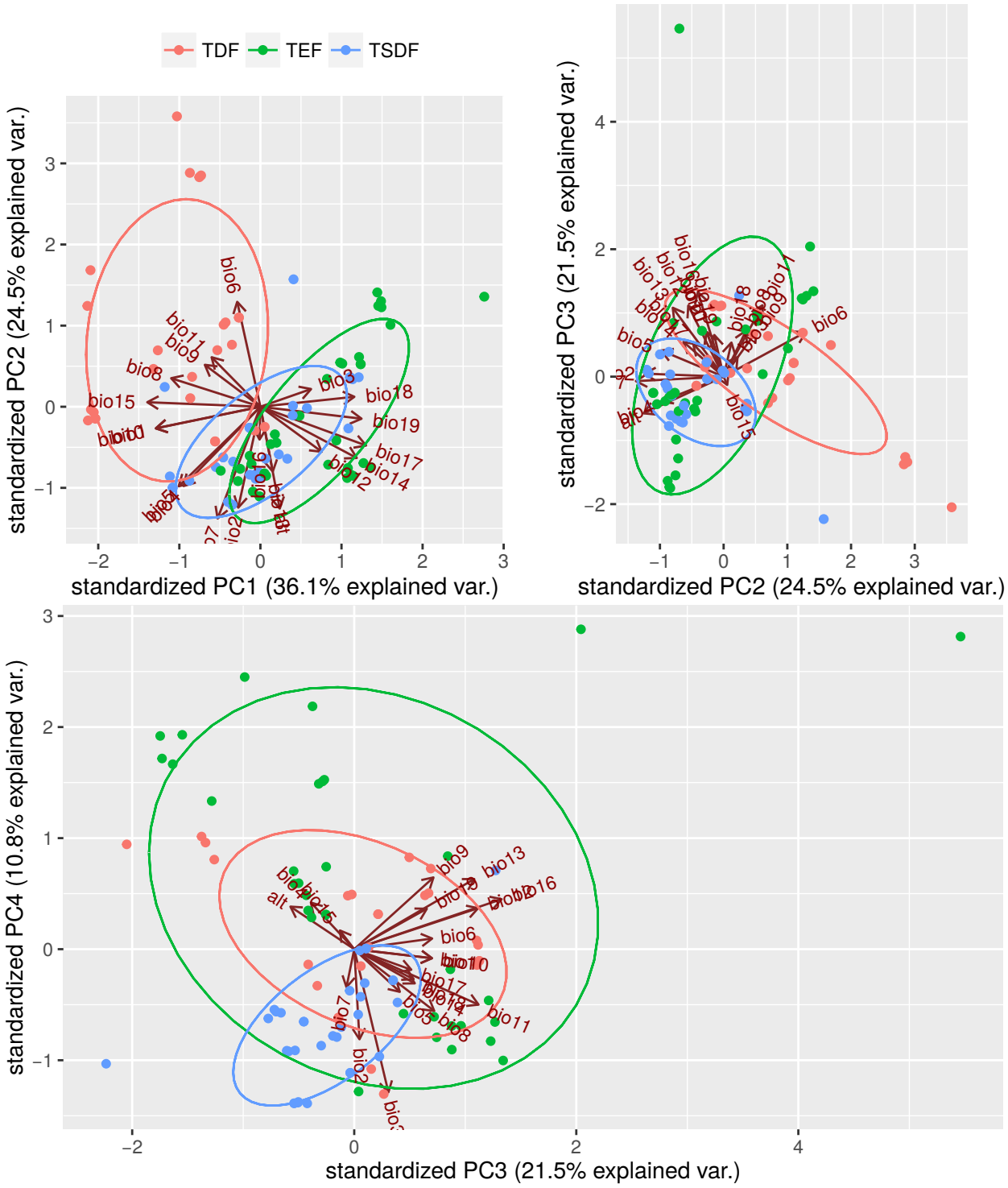

Table 1. Principal Component Analysis (PCA) values of summary statistics, rotations and scores, with 18 WorldClim bioclimatic variables of the Yucatan peninsula at each point were a Yucatan jay social group were found.

SUMMARY STATISTICS

```
## Importance of components:
##                            PC1    PC2    PC3    PC4     PC5     PC6     PC7
## Standard deviation     2.6863 2.2121 2.0755 1.4702 0.67621 0.55451 0.49279
## Proportion of Variance 0.3608 0.2447 0.2154 0.1081 0.02286 0.01537 0.01214
## Cumulative Proportion  0.3608 0.6055 0.8209 0.9290 0.95181 0.96718 0.97933
##                            PC8    PC9    PC10    PC11    PC12    PC13
## Standard deviation     0.37923 0.2900 0.26338 0.20892 0.16042 0.13285
## Proportion of Variance 0.00719 0.0042 0.00347 0.00218 0.00129 0.00088
## Cumulative Proportion  0.98652 0.9907 0.99419 0.99637 0.99766 0.99854
##                           PC14    PC15    PC16    PC17    PC18    PC19
## Standard deviation     0.1001 0.09680 0.07405 0.05290 0.03323 0.02067
## Proportion of Variance 0.0005 0.00047 0.00027 0.00014 0.00006 0.00002
## Cumulative Proportion  0.9990 0.99951 0.99978 0.99992 0.99998 1.00000
##                           PC20
## Standard deviation     6.3e-17
## Proportion of Variance 0.0e+00
## Cumulative Proportion  1.0e+00
```

ROTATIONS

```
##                PC1         PC2         PC3         PC4          PC5
## alt    0.058266130 -0.37278379 -0.18204623  0.17123900 -0.011813018
## bio10 -0.315444683 -0.07912011  0.22169194 -0.03647931 -0.099463811
## bio11 -0.147192984  0.18121598  0.35446114 -0.22324208 -0.047057466
## bio12  0.184954558 -0.16476446  0.35315855  0.16495999  0.099343888
## bio1  -0.315444683 -0.07912011  0.22169194 -0.03647931 -0.099463811
## bio13  0.037211712 -0.23716268  0.34221096  0.28217829  0.160371695
## bio14  0.290568215 -0.18760907  0.17271025 -0.13775500 -0.198097230
## bio15 -0.341305281  0.01658230 -0.04090754  0.07534939  0.472299563
## bio16 -0.002606818 -0.12000184  0.42025703  0.20117769  0.304472316
## bio17  0.318653438 -0.14199247  0.16271985 -0.08286998 -0.205183557
## bio18  0.283362039  0.03643754  0.16937807 -0.12076989  0.497755110
## bio19  0.304919296 -0.04373569  0.20702899  0.16273045 -0.206133315
## bio2  -0.066950173 -0.36938857  0.01496824 -0.36253426 -0.033757379
## bio3   0.152727812  0.06481095  0.09744626 -0.57588271  0.004391799
## bio4  -0.232052270 -0.29031312 -0.12380001  0.18781871 -0.036892341
## bio5  -0.246487071 -0.29118266  0.12993816 -0.17179198 -0.043516928
## bio6  -0.069950302  0.38404612  0.22222246  0.04288019  0.001722508
## bio7  -0.129175988 -0.40905867 -0.02219943 -0.15285716 -0.045208290
## bio8  -0.269246361  0.10440764  0.22823627 -0.24880057 -0.007088201
## bio9  -0.167673935  0.15351162  0.22594025  0.28864475 -0.498394298
##                PC6          PC7         PC8          PC9         PC10
## alt    0.006300824  0.192492975 -0.63307559  0.36840653 -0.35950898
## bio10  0.153177822 -0.262221506 -0.17695745 -0.14964490  0.03538716
## bio11  0.192943164  0.120595736 -0.30850769 -0.03248006  0.01932596
## bio12  0.028173783  0.145641514  0.21478761  0.01863726 -0.03245700
## bio1   0.153177822 -0.262221506 -0.17695745 -0.14964490  0.03538716
```

```
## bio13  0.006367593  0.143559026 -0.19388282 -0.18686219  0.03735468
## bio14  0.031231564  0.033548471 -0.10685895  0.22236258  0.42452595
## bio15 -0.162792624  0.205863189 -0.08077559 -0.11056490 -0.08344252
## bio16 -0.007397108  0.256032402  0.32705688  0.12896730  0.01252504
## bio17  0.069350409 -0.122600211  0.03565031  0.15197695  0.13339813
## bio18 -0.406630503 -0.584799582 -0.26257352  0.03908028  0.07233124
## bio19  0.168718473 -0.219464759  0.07323524 -0.27964382 -0.63204440
## bio2  -0.162236856  0.092454508  0.11386279 -0.11227784 -0.01995100
## bio3  -0.232804479  0.255378929 -0.03051796 -0.32063731 -0.30587407
## bio4  -0.043899395 -0.391405993  0.24375655 -0.08436513 -0.06737065
## bio5   0.093328036  0.018484478 -0.04222885 -0.04271340  0.08466927
## bio6   0.219287456  0.016317010 -0.13190084  0.02604452  0.07072964
## bio7  -0.099189713  0.001792231  0.09292596 -0.02026574  0.08043405
## bio8  -0.049700183 -0.141752157  0.22261935  0.69013223 -0.37076863
## bio9  -0.732983632  0.084549769 -0.08067324 -0.01773207  0.03116548
##              PC11        PC12         PC13         PC14        PC15
## alt   -0.06507747  0.26844778  0.108010328  0.035638420 -0.01095736
## bio10 -0.02668324  0.04506067  0.223867268  0.100099539  0.23134769
## bio11 -0.17242540 -0.05873610 -0.239668414  0.198181711  0.06972372
## bio12 -0.26177933  0.16657469  0.006061388 -0.341032386  0.05365496
## bio1  -0.02668324  0.04506067  0.223867268  0.100099539  0.23134769
## bio13  0.21370252 -0.57840862  0.128329172  0.095001084 -0.45822785
## bio14  0.44341276 -0.05430385  0.219759505 -0.378714585  0.32863427
## bio15  0.52448850  0.05119720 -0.362194651 -0.072910138  0.34257520
## bio16 -0.11394672  0.30819291  0.203042834  0.298528260  0.15644927
## bio17  0.30513697  0.20698926 -0.418292857  0.560873365 -0.11081439
## bio18 -0.16337104  0.04917390 -0.059350988 -0.065441885 -0.03063091
## bio19  0.10663965 -0.07572981 -0.237779082 -0.190909466  0.22871897
## bio2  -0.07654768 -0.01099195 -0.168359429 -0.008783901  0.03719086
## bio3   0.19705339  0.18963128  0.383035656  0.060749961 -0.16356683
## bio4   0.31914934  0.29260422  0.200071529  0.031305549 -0.27332419
## bio5  -0.10435639  0.14329455 -0.311886308 -0.368111104 -0.31314690
## bio6   0.17057480  0.41862147 -0.078764354 -0.276872112 -0.38896873
## bio7  -0.17614692 -0.06856395 -0.177006288 -0.021744102  0.00123392
## bio8   0.12698989 -0.28385217  0.046528773 -0.056766692 -0.08504479
## bio9  -0.02948810  0.06182471 -0.079723139 -0.017637264  0.01797674
##              PC16         PC17         PC18         PC19          PC20
## alt    0.003691240  0.005111904  0.050547354 -0.015350314 -1.439476e-16
## bio10  0.116815301 -0.236250706  0.028404305  0.003535883  7.071068e-01
## bio11 -0.004520611  0.695126940 -0.037973644 -0.001530234  2.775558e-16
## bio12  0.694058176  0.075978715  0.046428926  0.046512297  7.008283e-16
## bio1   0.116815301 -0.236250706  0.028404305  0.003535883 -7.071068e-01
## bio13  0.008368671 -0.054209035  0.079237576 -0.019624061 -1.387779e-17
## bio14 -0.158759177  0.155265944 -0.023271174  0.001115213 -5.689893e-16
## bio15  0.145174927 -0.033094018 -0.024867890  0.062189300 -3.261280e-16
## bio16 -0.462927400 -0.030324222 -0.078874826 -0.046976525 -7.424616e-16
## bio17  0.239461166 -0.199792137 -0.070118685  0.029889403  4.440892e-16
## bio18 -0.076440154  0.020556871 -0.008550669 -0.010515104  3.469447e-17
## bio19 -0.265394726  0.005155508  0.005606211  0.026576187 -6.453171e-16
## bio2  -0.064082899 -0.018919266  0.572589062 -0.545278792  4.718448e-16
## bio3   0.092378715 -0.030556137 -0.164068686  0.162067320 -4.440892e-16
## bio4   0.054361721  0.525265220 -0.001049831 -0.040733158  1.387779e-16
## bio5  -0.170732129 -0.170996349 -0.580214425 -0.170401995 -7.077672e-16
## bio6  -0.148528432 -0.143432878  0.478343152  0.122534708  2.220446e-16
```

```
## bio7  -0.158049106  0.012514510  0.229083227  0.787131314  2.220446e-16
## bio8   0.065905127 -0.052024077  0.009058449  0.015366118  1.665335e-16
## bio9  -0.023613535 -0.008535433 -0.027436280 -0.016892477 -2.498002e-16
```

SCORES

```
##               PC1         PC2         PC3          PC4           PC5
##  [1,] -0.71243600  2.43218539  0.44646384  0.463358917  1.2052320825
##  [2,] -1.21758145  2.23742252 -0.12078787  0.708251398  0.0144915976
##  [3,] -1.15501190  2.29926126 -0.04540695  0.724337318 -0.0056136288
##  [4,] -3.39872677  1.53863415  1.32188176  0.712490965  0.0166358382
##  [5,] -3.54366765  1.03164912  1.38938033  0.741522407  0.0551616988
##  [6,] -5.73266949  2.74968900  1.43062203  1.066913858  0.4892291250
##  [7,] -5.62947360  3.72418188  1.02924970  1.214915600  0.4981654360
##  [8,] -5.52015844 -0.15180715  2.29292238 -0.210157585 -0.3058629312
##  [9,] -5.71226159 -0.37386785  2.28716918  0.116378642 -0.2915627228
## [10,] -5.46939406 -0.32258257  2.33753948 -0.154911600 -0.2685596632
## [11,] -5.46939406 -0.32258257  2.33753948 -0.154911600 -0.2685596632
## [12,] -5.61439493 -0.07564068  2.31558152  0.056043703 -0.1768064698
## [13,] -2.26286719  0.81599167  0.26938467  0.024227031 -0.3266828395
## [14,] -1.50051403 -0.94561246 -0.29701244 -0.906383673  0.0722731349
## [15,]  0.47937868 -0.75263407  1.49336081 -0.894706847  0.6503918700
## [16,]  2.20772918  0.75944096  1.53995080 -1.167077935 -0.8072765548
## [17,]  2.64333440  1.20564095  1.82425020 -1.329458224 -0.8375416417
## [18,]  2.71227685  1.17539912  1.82185433 -1.016959125 -0.7885406135
## [19,]  3.32161211  1.16094190  1.99470384 -1.016116034 -0.4429155187
## [20,]  0.18936282 -1.88229231 -0.66279767  2.189017756 -0.2614269112
## [21,]  0.13725092 -1.83564104 -0.55967591  2.242857197 -0.2540423926
## [22,]  2.89816890 -1.67145503 -3.21462803  2.837711049 -0.0378551026
## [23,]  3.06976871 -1.88267012 -3.59310181  2.524024019  0.0726414579
## [24,]  2.24647416 -1.57936654 -2.66452960  1.960992191 -0.3229364645
## [25,]  0.53330931 -0.98182526 -1.13250324  1.033382027 -1.0429142508
## [26,]  0.34591802 -1.02064273 -1.03938535  0.873489793 -1.0237526778
## [27,] -0.74219864 -2.02765774 -0.79844074  0.420209324  0.3529862038
## [28,] -0.24987256 -2.31486066 -0.89667918  0.713163034  0.2755280765
## [29,] -0.02684616 -2.44548283 -0.52936662  0.457718039  0.3638529736
## [30,] -0.34768279 -1.85369616  0.07409858 -0.865360051 -0.0304851156
## [31,] -0.01339499 -1.94084766 -0.39834104 -1.148166020 -0.0457659558
## [32,] -0.05222819 -1.78687101 -0.61774418 -1.277070530 -0.2905041097
## [33,] -0.15131695 -1.83541026 -1.26129069 -1.343840084 -0.3587785216
## [34,] -0.17735947 -1.89900637 -1.60737805 -0.917395629 -0.0843240404
## [35,] -1.47754191 -1.64358171 -1.36962318 -0.842115105  0.2129378247
## [36,] -1.23582515 -1.38036745 -0.94307178 -0.959403734 -0.0077599996
## [37,] -0.90256691 -1.49723445 -1.46045400 -0.827505497  0.2302437839
## [38,]  0.16912009 -1.41584893 -1.49409803 -0.800300155  0.1767476853
## [39,]  0.60982500 -1.29901538 -1.22687694 -1.353489327 -0.1484161659
## [40,]  0.89155256 -1.41895911 -1.10589863 -1.340453955 -0.1125644211
## [41,] -0.35815336 -0.57370298 -0.07527333 -1.636317482 -0.2000321302
## [42,] -1.07136104 -2.59701268  0.10266833 -0.018228493  0.2257230231
## [43,] -0.93575756 -2.67259867  0.22112764  0.008709617  0.1641622141
## [44,] -3.00029102 -1.89980980  0.80850222 -0.705573884  0.2816061445
## [45,] -2.90687388 -2.20650997  0.72585231 -0.412422710  0.2777580928
## [46,] -3.16954146  0.53984280  2.64491717  1.042572399 -0.3792807953
## [47,] -0.71243600  2.43218539  0.44646384  0.463358917  1.2052320825
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## [48,] -1.50051403 -0.94561246 -0.29701244 -0.906383673  0.0722731349
## [49,] -2.33679614  6.37863944 -2.78013308  1.410932974  0.5872189476
## [50,] -2.76518399  7.91957632 -4.25363914  1.387725492 -0.0815026763
## [51,] -2.02535416  6.26029189 -2.85430901  1.491205847  0.5661746432
## [52,] -1.96640909  6.30759283 -2.61668473  1.185848147  0.6351803635
## [53,]  0.14221617 -0.54845652  0.55222125 -1.917621023  1.0661997744
## [54,] -0.94388315  1.69125812 -0.69025329 -0.483678268 -0.9429457788
## [55,] -1.42772696  1.54233462 -0.86065430 -0.202108861 -0.9993593842
## [56,] -2.32298988  0.23237457  0.12320367 -0.223566334 -0.4653495780
## [57,] -0.18763655 -0.65002303  0.31787131 -1.586999074  0.1808243604
## [58,] -0.66962012 -1.69359706 -0.52456273  1.091361445 -0.9301151119
## [59,]  3.32161211  1.16094190  1.99470384 -1.016116034 -0.4429155187
## [60,] -0.29446063 -1.56197964 -1.12048925  0.865494823 -0.8097892188
## [61,] -0.02684616 -2.44548283 -0.52936662  0.457718039  0.3638529736
## [62,]  0.13323042 -1.81623499 -0.59230475  2.220507181 -0.2741690224
## [63,]  3.26745782  1.35675653  0.08188734 -1.884285117 -0.0005229851
## [64,]  3.87274820  3.11794847  2.78395671 -1.473745218 -0.5098787761
## [65,]  4.00949944  2.71286371  2.55129379 -1.217418109 -0.4964101564
## [66,]  1.29391534 -0.24784193  1.79780442 -0.266688381 -1.0819898528
## [67,]  3.41390629 -1.53656517 11.33626107  4.137912909 -0.2070980994
## [68,]  7.41666694  3.00194173  4.23864995  4.234455408  0.9888317975
## [69,]  4.30834895  2.23308748  0.92117906 -0.853620085 -0.8185127500
## [70,] -1.31575998 -1.74551129  1.74810708  1.231567188  0.6139143967
## [71,]  2.87494648 -1.94222485 -3.39344072  2.449241279 -0.1346336785
## [72,]  2.99153958 -1.85425967 -3.62795856  2.822670565  0.0305254252
## [73,]  3.65880752 -1.65194207 -2.04817881  3.602525001  0.2807357975
## [74,]  2.51516887 -0.91964368 -0.77980101  3.214661305 -0.0919750423
## [75,]  3.99613963  2.87956766  2.63133532 -0.964390690 -0.5613654038
## [76,]  3.90542700  2.75221892  2.51289379 -0.678615468 -0.8222691133
## [77,] -0.35546528 -1.33842403 -0.86159419  0.511859762 -0.8812270545
## [78,] -1.23582515 -1.38036745 -0.94307178 -0.959403734 -0.0077599996
## [79,] -0.35815336 -0.57370298 -0.07527333 -1.636317482 -0.2000321302
## [80,] -0.93575756 -2.67259867  0.22112764  0.008709617  0.1641622141
## [81,] -2.90687388 -2.20650997  0.72585231 -0.412422710  0.2777580928
## [82,]  1.07799553  0.02545204  0.11888782 -0.629947488  1.3621662228
## [83,]  1.09726782  3.47516525 -4.63859394 -1.516906679 -2.7851066879
## [84,]  2.91601680 -0.59117859  0.46980728 -1.421198583  1.9454149186
## [85,]  3.25682449  0.80491956 -0.87858016 -2.041965796  0.7489528669
## [86,]  1.54256984 -0.03538308  0.19660035 -0.449531488  1.1607897623
## [87,]  2.96782730  0.80255219 -1.12353708 -2.040175299  0.8406432280
## [88,] -0.15682324 -1.96520099 -0.32594075 -1.163735640 -0.1071332477
## [89,] -2.35364382 -2.01737603 -0.24101822 -1.030735335  0.1382205691
## [90,]  1.07023132 -0.23470328 -0.08573249 -0.549841268  1.3542595288
## [91,]  3.05357964  0.75064700 -1.04616245 -2.022347128  0.8491081728
## [92,]  3.02866980  0.77076595 -1.05293330 -2.031776638  0.8639718039
## [93,]  2.96782730  0.80255219 -1.12353708 -2.040175299  0.8406432280
##                PC6          PC7         PC8          PC9         PC10
##  [1,] -0.802764277 -0.504665431 -0.23399118  0.014083022  0.061512052
##  [2,] -0.057915228  0.929078492  0.41621421 -0.137917527 -0.053480762
##  [3,] -0.015316383  0.930580681  0.39673005 -0.119406138 -0.035732998
##  [4,] -0.059362596 -0.220108187  0.26808182  0.227451557 -0.061606449
##  [5,] -0.130298621 -0.273170077  0.12813706  0.261588671 -0.150927904
##  [6,]  0.192256864  0.174517912  0.56280832 -0.110140228  0.115104172
##  [7,]  0.286754455  0.385124315  0.85101629 -0.367900505  0.157297239
```

```
##  [8,] -0.501490287 -0.079737762 -0.03409957  0.125608090  0.081209922
##  [9,] -0.369255384 -0.246937415 -0.15225142  0.151890315  0.254354705
## [10,] -0.511962901 -0.040574513 -0.10015582  0.023608028  0.085401112
## [11,] -0.511962901 -0.040574513 -0.10015582  0.023608028  0.085401112
## [12,] -0.393898086 -0.082830784 -0.06821199  0.161781507  0.304656370
## [13,] -0.344077259  0.464801840  0.61179480 -0.086625071  0.156607598
## [14,]  0.600315488  0.162652680  0.34527221  0.060801284  0.457755412
## [15,]  0.223058106  1.117756292  0.19070530  0.058334444  0.036111125
## [16,] -0.653654753  0.242279379 -0.47077239  0.306838194 -0.114779670
## [17,] -0.681681602  0.035568244 -0.34614129  0.099103749 -0.148211222
## [18,] -0.586336322 -0.054956431 -0.42920808  0.136784472  0.002861823
## [19,] -0.688687352  0.051554846 -0.46298525  0.159581997 -0.265083617
## [20,] -0.265522470  0.210756711 -0.09649852 -0.250032609  0.119308461
## [21,] -0.209961506  0.137524174 -0.17236499 -0.279331748  0.124252455
## [22,] -0.342340379 -0.338671061  0.42084336  0.107809311  0.007717675
## [23,] -0.480150928 -0.130986446  0.51930890 -0.109301868 -0.127370741
## [24,] -0.384543460  0.100614008  0.30911817  0.504502617 -0.093263712
## [25,] -0.166503741 -0.138026788 -0.15087513  0.527446226  0.050108000
## [26,] -0.238894671  0.103474728 -0.26299967  0.526869627  0.172132163
## [27,]  0.624680924 -0.269938672 -0.76323015 -0.249230169  0.614910574
## [28,]  0.555026764 -0.376835242 -0.57992775 -0.455468022  0.205217939
## [29,]  0.446629034 -0.213863892 -0.67270856 -0.566047671  0.036109180
## [30,]  0.524183392 -0.353985500  0.67009342  0.029670256  0.384694466
## [31,]  0.424505113  0.041647699  0.20664022 -0.007106221  0.093819645
## [32,]  0.392796666 -0.003534409  0.18428808  0.039502842  0.108424394
## [33,]  0.371194875  0.088267623  0.14744622  0.196293034  0.007495503
## [34,]  0.261222496  0.296563162 -0.02468188 -0.046470729 -0.554052800
## [35,]  0.247037566  0.250110620 -0.24431216  0.154860668  0.080410789
## [36,]  0.333182608  0.206305783 -0.23814207 -0.125992252 -0.579778545
## [37,]  0.241730502  0.614347360 -0.56176784 -0.563516705  0.299650491
## [38,]  0.327554770  0.713754382 -0.32689137 -0.401243027  0.328308130
## [39,]  0.292964675  0.862970377 -0.14639434  0.094775548 -0.065548127
## [40,]  0.226083564  0.941078521  0.01567647  0.119129511 -0.130285676
## [41,]  0.401398265  0.720235577  0.03334246 -0.062603696 -0.058772211
## [42,]  0.465137218 -0.626072522 -0.24791126  0.056385818 -0.325597232
## [43,]  0.501516720 -0.648871391 -0.20812780  0.103129694 -0.333829612
## [44,]  0.329336809 -0.392217772 -0.14784949 -0.263238627 -0.679063440
## [45,]  0.438116588 -0.611862754 -0.08783011 -0.036404424 -0.559880626
## [46,]  0.003638303 -0.153285708  0.26270551 -0.019066278  0.060017681
## [47,] -0.802764277 -0.504665431 -0.23399118  0.014083022  0.061512052
## [48,]  0.600315488  0.162652680  0.34527221  0.060801284  0.457755412
## [49,]  0.403591574 -0.169375661 -0.54231414  0.221165270  0.039088209
## [50,]  0.876511639 -0.167745512 -0.47450272  0.023370777 -0.096966450
## [51,]  0.435476593 -0.185805856 -0.47517855  0.296585941 -0.075791485
## [52,]  0.248452580  0.064285664 -0.57175491  0.170731727 -0.157468675
## [53,] -0.535089408 -0.623737123  0.15258397 -0.042093000 -0.333110279
## [54,] -0.234329048  0.448088947  0.41042474 -0.018370792 -0.210225383
## [55,] -0.078732880  0.136398326  0.30832438  0.018372435 -0.099564725
## [56,] -0.479215023  0.404766856  0.45904654  0.020058991  0.267015601
## [57,]  0.181339849  0.492670740  0.82098258 -0.097020456 -0.447743868
## [58,] -0.508664928 -0.307388103 -0.73609837 -0.579963889  0.265709108
## [59,] -0.688687352  0.051554846 -0.46298525  0.159581997 -0.265083617
## [60,] -0.658965233 -0.006713735 -0.24567847  0.548336909  0.222409834
## [61,]  0.446629034 -0.213863892 -0.67270856 -0.566047671  0.036109180
```

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## [62,] -0.210254111  0.117330721 -0.17629109 -0.283172324  0.126783630
## [63,]  0.201518044 -0.282290045 -0.02185718  0.442735783  0.276293251
## [64,] -0.353395947 -0.245750774  0.28136446 -0.756794809  0.435060101
## [65,] -0.374917685 -0.070551207 -0.27382004 -0.538440157  0.153164985
## [66,] -0.158700213  1.226168392  0.24888389  0.274674028 -0.178313709
## [67,]  1.603485687 -1.231002535  0.39797229  0.372203282  0.204800568
## [68,]  1.244983189  1.144117649  0.15943993 -0.345167670 -0.659303400
## [69,] -0.114787748  0.133788208 -0.42021866  0.031659737 -0.149377957
## [70,] -0.813834469  0.682310401  0.08298492 -0.075548902 -0.246180418
## [71,] -0.514667273 -0.128785684  0.40000585 -0.155568941 -0.030725402
## [72,] -0.450029693 -0.291510123  0.53371931  0.034418852  0.019196656
## [73,] -0.010931670  0.261952010  0.17862846  0.110603687  0.204400041
## [74,]  0.170739453  0.175701617 -0.32266244  0.363120178  0.160315894
## [75,] -0.068649638 -0.217112070 -0.27554224 -0.293143992  0.161530691
## [76,]  0.063295435  0.030048366 -0.30030747 -0.196776084 -0.032407032
## [77,] -0.577653058  0.107307759 -0.39975650  0.339257705  0.144345187
## [78,]  0.333182608  0.206305783 -0.23814207 -0.125992252 -0.579778545
## [79,]  0.401398265  0.720235577  0.03334246 -0.062603696 -0.058772211
## [80,]  0.501516720 -0.648871391 -0.20812780  0.103129694 -0.333829612
## [81,]  0.438116588 -0.611862754 -0.08783011 -0.036404424 -0.559880626
## [82,] -1.544162586 -0.517374461  0.30188699 -0.168108300 -0.149438709
## [83,]  0.758510127 -1.798690515  1.03954463 -0.831300536 -0.147289962
## [84,]  0.071076243  0.539372750  0.02318022 -0.433884110  0.585660854
## [85,]  0.540447960 -0.324408177  0.15985512  0.450267732  0.196462386
## [86,] -1.459061018 -0.669864904  0.40911404 -0.115479686 -0.084794748
## [87,]  0.452008841 -0.374940919  0.21675964  0.364162986  0.145981470
## [88,]  0.349831842 -0.001664851  0.32744084  0.055670470  0.093902857
## [89,]  0.382146908  0.022901008 -0.17577277  0.319238365  0.167003071
## [90,] -1.737616092 -0.472214724  0.26026801 -0.254723930 -0.145873443
## [91,]  0.456457895 -0.335373094  0.15996005  0.405081151  0.144474966
## [92,]  0.448327290 -0.331311974  0.17805837  0.398735630  0.173377936
## [93,]  0.452008841 -0.374940919  0.21675964  0.364162986  0.145981470
##               PC11         PC12         PC13         PC14          PC15
##  [1,]  0.231635609  0.251811563  0.080120782 -0.111763534 -0.1514087645
##  [2,]  0.521423344  0.102272201  0.060014452  0.080611417 -0.0231794509
##  [3,]  0.470624069  0.124576432  0.104656292  0.061121517 -0.1039601633
##  [4,] -0.228969903  0.227604415 -0.216536024  0.017200370 -0.1322736911
##  [5,] -0.307702299  0.292126367 -0.091347329  0.109416449 -0.0960363029
##  [6,] -0.420497147 -0.164907632  0.130536470 -0.126027101  0.1439143523
##  [7,] -0.436388604 -0.389573565  0.120035302 -0.207903248  0.0798039579
##  [8,] -0.034416178 -0.081302834  0.118451406  0.006351448 -0.0614693331
##  [9,] -0.162571696 -0.016837648  0.077989312 -0.020492957  0.0158273671
## [10,] -0.087783620 -0.008860255  0.086590090 -0.025369931 -0.0894607675
## [11,] -0.087783620 -0.008860255  0.086590090 -0.025369931 -0.0894607675
## [12,] -0.220842228 -0.093279588 -0.070207293 -0.038423878  0.1431016257
## [13,]  0.431127668  0.050492349  0.068674570 -0.011854592  0.0640869412
## [14,]  0.325710945 -0.122663733  0.068319908 -0.064473686  0.0008216903
## [15,] -0.208489194 -0.169581544 -0.085638486  0.088520064 -0.2347597190
## [16,] -0.264663880 -0.208135168 -0.134037370  0.059182939 -0.0162551500
## [17,] -0.054175496 -0.144454618  0.062270784  0.017421049 -0.0773767719
## [18,] -0.186369735 -0.183073835 -0.111365551 -0.013920814  0.0126589938
## [19,] -0.043963340 -0.127256977  0.115553344  0.033222933 -0.0662210094
## [20,] -0.097805634 -0.123680344  0.023136274  0.132550288 -0.0174054730
## [21,] -0.098009216 -0.128381066  0.153069648  0.209392074  0.0844335175
```

```
## [22,] -0.194865574  0.051210838 -0.078301663 -0.096453434 -0.0258096115
## [23,] -0.181817680  0.069524346  0.045322859 -0.013378389 -0.1312054821
## [24,] -0.049054528 -0.203985870 -0.155580341 -0.086830273 -0.0548336608
## [25,]  0.140248487 -0.118634585  0.041560556 -0.029250363  0.0575497152
## [26,]  0.055980009 -0.184837145 -0.140330611 -0.032500622  0.0863494103
## [27,]  0.047490594  0.028613147 -0.101261891  0.112385271 -0.1333461626
## [28,]  0.203797207 -0.052024944 -0.174458907 -0.029936279  0.0409499559
## [29,]  0.243494318  0.041695377 -0.088145892  0.026497986  0.0240376034
## [30,]  0.228940644 -0.198638045 -0.042630612 -0.020261262 -0.0991621234
## [31,] -0.073938498  0.056845066  0.087740166 -0.019670401 -0.0105212889
## [32,] -0.196545799  0.128188824  0.074908548 -0.092251133  0.0734180469
## [33,] -0.219779918  0.196258371  0.121269928 -0.156865049  0.0323145761
## [34,]  0.021395394  0.077355683  0.002222609 -0.192823857  0.1263151448
## [35,] -0.102144632 -0.050981870  0.118032076  0.003882595 -0.0598703786
## [36,]  0.112505866 -0.048720925  0.027960431 -0.168331256 -0.0265357714
## [37,] -0.238034792  0.263956276  0.144656493  0.089094443 -0.1311401355
## [38,] -0.258936339  0.254240108 -0.043563723 -0.026329017 -0.1505828025
## [39,] -0.109794188  0.134578973  0.002478152 -0.143256385 -0.0314903018
## [40,] -0.100264251  0.084504172 -0.156122795 -0.138111965  0.0285050869
## [41,] -0.171985236 -0.024578062 -0.337523148 -0.099040157 -0.1189881512
## [42,]  0.246942631 -0.104178341  0.097753263 -0.014174501  0.0167242748
## [43,]  0.225229268 -0.047697724  0.141203574 -0.012708683  0.0344106181
## [44,] -0.076931170 -0.163996540 -0.020252680  0.122559464 -0.0316706623
## [45,] -0.101961150 -0.191679738 -0.039881429  0.100427213  0.0198165549
## [46,]  0.168051982  0.205582259 -0.131543213  0.183686172  0.2586372234
## [47,]  0.231635609  0.251811563  0.080120782 -0.111763534 -0.1514087645
## [48,]  0.325710945 -0.122663733  0.068319908 -0.064473686  0.0008216903
## [49,] -0.030677763  0.062038641 -0.112306737  0.032464138  0.1458014093
## [50,]  0.075854168 -0.245795767  0.059271042  0.033828623 -0.1121514981
## [51,] -0.060937940  0.032478665 -0.094346470 -0.007849329 -0.0478830134
## [52,] -0.025663278  0.094957812 -0.068615649  0.096088703 -0.0397586978
## [53,] -0.317798633  0.307299957  0.036928813  0.018059636  0.0984781245
## [54,]  0.240744388  0.272055035 -0.270685743  0.136897447 -0.0242845904
## [55,]  0.252337688  0.302395432 -0.180520118  0.013529287  0.1615273716
## [56,]  0.505997502  0.060849212 -0.042183250 -0.069183160  0.0292742944
## [57,]  0.143364060  0.202926064  0.131203304  0.149337573  0.0637519530
## [58,]  0.103375115  0.088804606 -0.302533614 -0.057759662  0.2531302254
## [59,] -0.043963340 -0.127256977  0.115553344  0.033222933 -0.0662210094
## [60,]  0.211304541 -0.159616442 -0.070400080 -0.033266587 -0.0022896643
## [61,]  0.243494318  0.041695377 -0.088145892  0.026497986  0.0240376034
## [62,] -0.096098322 -0.127939631  0.138398476  0.196567952  0.0921379433
## [63,] -0.055296542 -0.004963238 -0.193800223 -0.131157753  0.2382112826
## [64,]  0.001633264 -0.260992047  0.037569275 -0.065852462  0.0495186469
## [65,] -0.045069901  0.027362749  0.174530568 -0.063393633  0.0299113041
## [66,]  0.091600375 -0.148493945 -0.041425945  0.390480018 -0.0534266631
## [67,]  0.002149047  0.298077648 -0.206311841 -0.036095568 -0.1765833739
## [68,]  0.232745362 -0.253289101 -0.075826979 -0.122966941  0.1226924103
## [69,] -0.092820703  0.540425033  0.135773041 -0.079739702  0.0935168260
## [70,] -0.482535038  0.233581669  0.105226276  0.097616469  0.2420938887
## [71,] -0.185819585  0.084967114  0.025171060  0.016810696 -0.0328675913
## [72,] -0.265082703  0.016744801 -0.122336526 -0.053964076 -0.0560691459
## [73,] -0.070269763  0.062985176  0.367565555 -0.015980010  0.0104958314
## [74,] -0.143911956  0.015618047  0.183753800 -0.023161820  0.0180599097
## [75,] -0.112809183 -0.091266519  0.125233559 -0.052364007  0.0100377986
```

```
## [76,]  0.060089352  0.083196665  0.260396554 -0.069199341 -0.0770906628
## [77,]  0.247510717 -0.030148541  0.023763018 -0.049134468 -0.0254604141
## [78,]  0.112505866 -0.048720925  0.027960431 -0.168331256 -0.0265357714
## [79,] -0.171985236 -0.024578062 -0.337523148 -0.099040157 -0.1189881512
## [80,]  0.225229268 -0.047697724  0.141203574 -0.012708683  0.0344106181
## [81,] -0.101961150 -0.191679738 -0.039881429  0.100427213  0.0198165549
## [82,]  0.163111317 -0.179259521 -0.165859187 -0.065332891 -0.1148092975
## [83,] -0.198365790 -0.009990677 -0.006459109  0.089464124 -0.0893554873
## [84,] -0.198373276 -0.082093721 -0.209587349  0.138779647  0.0729423324
## [85,] -0.041271768 -0.005588885  0.038124015  0.014397983  0.0869706564
## [86,]  0.308143028  0.057014276 -0.001943618  0.017480020  0.0162223959
## [87,] -0.018243138 -0.021922632  0.034278270  0.149462134  0.0381950187
## [88,] -0.016161397  0.018645274  0.085248468 -0.040457797 -0.1042258194
## [89,]  0.214006390  0.016803685  0.240514379 -0.024796397  0.0150264274
## [90,]  0.181627472 -0.179205843 -0.170311704 -0.037101681 -0.0069055310
## [91,] -0.017259909 -0.028366704  0.034952771  0.107500958  0.0720649893
## [92,] -0.021662831 -0.039915413  0.053277639  0.110947927  0.0697198618
## [93,] -0.018243138 -0.021922632  0.034278270  0.149462134  0.0381950187
##                PC16         PC17          PC18          PC19          PC20
##  [1,] -1.640018e-01 -0.020806502  0.0397970021 -0.0138734531 -2.830392e-16
##  [2,] -2.416859e-02  0.023859275  0.0171282415  0.0322005441 -3.652753e-16
##  [3,] -4.593764e-02 -0.013610814  0.0591454561 -0.0100210529 -3.331995e-16
##  [4,]  1.062197e-01 -0.047687760  0.0257811801  0.0291123802  3.089363e-16
##  [5,]  1.510354e-01  0.002517733  0.0429617797  0.0119738758  4.021055e-16
##  [6,]  4.000355e-02  0.020915639  0.0727233658  0.0121381734  5.085336e-16
##  [7,] -2.204526e-02  0.095166852  0.0520039858  0.0214011562  4.116778e-16
##  [8,]  3.123137e-02 -0.022240881 -0.0391690107  0.0304030358  3.011234e-18
##  [9,]  8.429586e-03  0.002276930  0.0142506639 -0.0250228789 -1.163155e-16
## [10,]  5.052547e-03 -0.013024337 -0.0211856262  0.0101773656 -9.909192e-17
## [11,]  5.052547e-03 -0.013024337 -0.0211856262  0.0101773656 -9.909192e-17
## [12,] -3.275322e-02  0.103385458 -0.0323037015  0.0063697311 -1.673132e-17
## [13,] -3.844928e-02 -0.033474421 -0.0169089125  0.0205976669 -2.984295e-16
## [14,] -4.596493e-03 -0.003544687  0.0176580183 -0.0190149164  2.907460e-16
## [15,] -7.888192e-02 -0.053810470  0.0210858629 -0.0103832529 -3.325608e-16
## [16,] -2.173005e-01  0.032699651 -0.0126480499  0.0009563097 -4.774537e-16
## [17,] -2.431332e-02  0.045116517  0.0038601330  0.0104490843 -3.503070e-16
## [18,] -4.065615e-02  0.027386451  0.0241816841 -0.0048744450 -2.801883e-16
## [19,]  1.149209e-01 -0.043588406  0.0380403056  0.0165662243 -3.468151e-16
## [20,] -1.079288e-01  0.021574704 -0.0120182839 -0.0055099327 -4.704722e-16
## [21,] -5.625963e-02 -0.061787588 -0.0135225792  0.0122813704 -4.727212e-16
## [22,]  6.957344e-02 -0.008246002  0.0315550606 -0.0112782923  2.987086e-16
## [23,]  7.532330e-02 -0.026594145 -0.0267940404  0.0174912629  1.023688e-16
## [24,] -2.335456e-02 -0.024546433  0.0213475515 -0.0212529658 -1.149363e-16
## [25,]  5.797740e-02  0.096669251  0.0091560637  0.0116110945  1.337919e-16
## [26,] -9.985718e-03  0.069846118  0.0172923040 -0.0154123800  1.013504e-16
## [27,]  1.514157e-01  0.024021964  0.0570358615 -0.0134230185  5.212223e-16
## [28,] -4.238702e-02 -0.040062357  0.0145981277  0.0232461018 -9.248030e-17
## [29,] -6.852543e-03  0.037423460  0.0284516026  0.0090605450 -2.928766e-16
## [30,]  4.000405e-02 -0.050217591 -0.0601665609 -0.0121376438  3.155748e-16
## [31,]  9.401669e-03 -0.063955426 -0.0254830741 -0.0340128260  1.628897e-16
## [32,] -8.853818e-04 -0.066989201 -0.0341695481 -0.0329242794  2.408443e-16
## [33,] -2.740573e-02 -0.016753714 -0.0640005443 -0.0153536841  2.680710e-16
## [34,] -1.277127e-01 -0.006256425 -0.0366036949  0.0143476346 -2.686957e-16
## [35,]  1.673356e-01 -0.022812643  0.0310634705 -0.0305345831  5.418951e-16
```

```
## [36,] -2.495191e-02  0.009855111  0.0040189567  0.0512099454 -1.138395e-16
## [37,]  1.250520e-01  0.115781791 -0.0173256203  0.0114370948  3.103223e-16
## [38,]  3.744264e-02  0.113448055 -0.0301137813  0.0151372513  2.302850e-16
## [39,] -3.214230e-02  0.003459222 -0.0031046802 -0.0015852362  2.336993e-17
## [40,] -1.021387e-01  0.053199558 -0.0303158727 -0.0069385231 -1.386451e-16
## [41,] -2.602719e-02 -0.108661688  0.0233514295  0.0031806541  1.836010e-16
## [42,]  3.476088e-02 -0.005727129  0.0221135755 -0.0118889581 -2.725612e-17
## [43,] -3.385715e-03  0.012218888  0.0149216840 -0.0179024643 -1.460178e-16
## [44,]  1.220893e-02  0.004595309 -0.0181828992  0.0247087252  2.128747e-17
## [45,] -2.239773e-02  0.011150956  0.0165683188 -0.0297383243  1.724268e-16
## [46,]  4.573606e-02 -0.087473527  0.0105644294  0.0125503761 -5.673828e-16
## [47,] -1.640018e-01 -0.020806502  0.0397970021 -0.0138734531 -2.830392e-16
## [48,] -4.596493e-03 -0.003544687  0.0176580183 -0.0190149164  2.907460e-16
## [49,] -3.395239e-02  0.032728327 -0.0321445954 -0.0231870792  9.719873e-16
## [50,]  1.122014e-01 -0.045869140 -0.1134512768  0.0112172470  1.546643e-15
## [51,] -9.039100e-02 -0.009719088 -0.0158610219 -0.0329954863  9.000438e-16
## [52,] -3.036959e-02 -0.011074161 -0.0420394339 -0.0133310957  7.792317e-16
## [53,] -8.216299e-02  0.023316640 -0.0356444223 -0.0168478928 -8.480465e-18
## [54,]  3.612252e-02  0.022151168  0.0227918664 -0.0032461977  2.637738e-16
## [55,]  4.146783e-02 -0.110250800  0.0427070227  0.0030474750  2.703205e-16
## [56,] -3.765769e-02  0.074951131 -0.0095996584 -0.0144423909 -2.013467e-16
## [57,]  7.705319e-02  0.157550830  0.0008079080 -0.0290903078 -5.312110e-17
## [58,] -6.376950e-02 -0.041239501 -0.0110238375 -0.0051583570 -4.035682e-16
## [59,]  1.149209e-01 -0.043588406  0.0380403056  0.0165662243 -3.468151e-16
## [60,]  7.547710e-02  0.077661434 -0.0177187193 -0.0255588432  7.965030e-17
## [61,] -6.852543e-03  0.037423460  0.0284516026  0.0090605450 -2.928766e-16
## [62,] -4.422759e-02 -0.059599791 -0.0137374576  0.0146494231 -4.457978e-16
## [63,]  1.453082e-01  0.023898495  0.0247133558  0.0228660220  5.950276e-16
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## [67,] -7.483395e-02  0.037661222 -0.0571369757  0.0168933835 -2.009999e-15
## [68,]  1.507971e-01  0.016181017 -0.0249430391 -0.0226879680 -2.052732e-15
## [69,]  4.981210e-02  0.102239040 -0.0094620843  0.0096078111 -4.835664e-16
## [70,]  4.217822e-02 -0.105867822 -0.0146645118 -0.0294250295 -8.747306e-16
## [71,]  6.572724e-02  0.014311528 -0.0251917625 -0.0027499103  2.343905e-16
## [72,]  4.909610e-02  0.010600638 -0.0099755837 -0.0077300956  2.523785e-16
## [73,] -1.367383e-01 -0.052489508  0.0264381009  0.0240322682 -5.415022e-16
## [74,] -1.223082e-01  0.037208218  0.0594611586  0.0288589471 -4.327225e-16
## [75,] -9.780795e-05  0.033089573  0.0272939379 -0.0464546127 -2.919415e-16
## [76,]  4.605934e-02 -0.035571704  0.0360760755 -0.0420532879 -4.503948e-16
## [77,]  8.741602e-02 -0.037552250 -0.0392945896  0.0278559874 -1.024530e-16
## [78,] -2.495191e-02  0.009855111  0.0040189567  0.0512099454 -1.138395e-16
## [79,] -2.602719e-02 -0.108661688  0.0233514295  0.0031806541  1.836010e-16
## [80,] -3.385715e-03  0.012218888  0.0149216840 -0.0179024643 -1.460178e-16
## [81,] -2.239773e-02  0.011150956  0.0165683188 -0.0297383243  1.724268e-16
## [82,]  3.904555e-02  0.050121071  0.0049340837 -0.0131190062 -1.796208e-16
## [83,] -9.678487e-02  0.029306715  0.0419777244 -0.0040819590  1.976025e-15
## [84,] -4.271771e-02  0.033048484  0.0033503261 -0.0106966041 -1.807859e-16
## [85,]  1.203573e-02 -0.076417839  0.0445048175  0.0075727629  4.368149e-16
## [86,]  9.523005e-03  0.027676753 -0.0442792644  0.0058452729 -3.327636e-16
## [87,] -3.300004e-02  0.017325309 -0.0005802681  0.0277518956  5.916309e-16
## [88,] -2.524818e-03 -0.025990480 -0.0669321647 -0.0126656129  1.428120e-16
## [89,]  4.114637e-02 -0.066661958 -0.0295462322 -0.0131461503  1.438969e-16
```

```
## [90,]  8.177556e-02 -0.013402090 -0.0257174145  0.0035096649 -2.521448e-16
## [91,] -2.281798e-04 -0.006451403  0.0053040854  0.0332084358  5.174840e-16
## [92,] -2.502197e-02 -0.003860376  0.0027619784  0.0300689257  5.124217e-16
## [93,] -3.300004e-02  0.017325309 -0.0005802681  0.0277518956  5.916309e-16
```

Table 2. Results of eighteen t-test comparing the two phases (*pre-reproductive* and *reproductive*) and years (2012-2013) on the social organization (group size, subadults and adults) for each of the three types of vegetations. Confidence level of 95%.

t*-test comparing *the two phases (*reproductive and pre-reproductive****) on the social organization***				
Social organization	Test statistic	df	P value	Vegetation type
Group size	0.93626	22.149	0.3592	Dry
Subadult	-1.1173	20.551	0.2767	
Adult	1.7594	19.174	0.09446	
Group size	-0.98969	21.576	0.3333	Subdeciduous
Subadult	-2.4788	19.613	0.0224	
Adult	-0.21383	22.637	0.8326	
Group size	-2.6568	16.317	**0.01702**	Evergreen
Subadult	-3.0843	16.55	**0.006892**	
Adult	-1.9071	18.07	0.07253	
t-test* comparing *year 2012 and 2013 on the social organization				
Group size	0.60178	21.872	0.5535	Dry
Subadult	-1.6429	20.597	0.1156	
Adult	2.0589	16.624	0.05553	
Group size	1.9399	21.02	0.06593	Subdeciduous
Subadult	-1.746	29.433	0.09125	
Adult	2.4335	19.713	**0.02461**	
Group size	-0.69214	22.027	0.4961	Evergreen
Subadult	-2.905	28.25	**0.007061**	
Adult	0.51657	20.632	0.6109	

Table 3. Summary statistics of ANOVA and Tukey HSD test comparing the Yucatan jay social organization (Group size, subadults and adults) at the *pre-reproductive* phase for the three vegetation types from the Yucatan peninsula tropical forests: Dry, Subdeciduous and Evergree

Group size					
	df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Vegetation type	2	250.3	125.15	7.517	**0.000957 *****
Residuals	90	1498.4	16.65		
Tukey HSD test					
	diff	lwr	upr	p adj	
Subdeciduous & Dry	-1.672727	-4.250987	0.90553250	0.2745090	
Evergreen & Dry	-4.057143	-6.603453	-1.51083302	**0.0007695**	
Evergreen & Subdeciduous	-2.384416	-4.743824	-0.02500722	0.0470349	
Subadults					
Vegetation type	2	26.57	31.283	9.608	**0.000165 *****
Residuals	90	293.05	3.256		
Tukey HSD test					
Subdeciduous & Dry	1.1187879	-2.258976	0.02140048	0.0556427	
Evergreen & Dry	-2.0685714	-3.194631	-0.94251234	**0.0000950**	
Evergreen & Subdeciduous	-0.9497835	-1.993189	0.09362176	0.0820701	
Adults					
Vegetation type	2	65.5	32.74	2.041	0.136
Residuals	90	1444.2	16.05		
Tukey HSD test					
Subdeciduous & Dry	-0.5539394	-3.085122	1.9772432	0.8610328	
Evergreen & Dry	-1.9885714	-4.488388	0.5112446	0.1458031	
Evergreen & Subdeciduous	-1.4346320	-3.750959	0.8816952	0.3072387	
Signif. codes: 0 ‘***’, 0.001 ‘**’, 0.01 ‘*’, 0.05 ‘.’, 0.1 ‘ ’ 1					

Table 4. Summary statistics of ANOVA and Tukey HSD test comparing the Yucatan jay social organization (Group size, subadults and adults) at the reproductive phase for the three vegetation types from the Yucatan peninsula tropical forests: Dry, Subdeciduous and Evergreen.

Group size					
	df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Vegetation type	2	74.4	37.21	1.599	0.218
Residuals	31	721.3	23.27		
Tukey HSD test					
Subdeciduous & Dry	0.8409091	-4.114863	5.796681	0.9086260	
Evergreen & Dry	3.4772727	-1.478499	**8.433045**	0.2113937	
Evergreen & Subdeciduous	2.6363636	-2.425996	7.698724	0.4158860	
Subadults					
Vegetation type	2	10.31	5.153	1.867	0.172
Residuals	31	85.58	2.761		
Tukey HSD test					
Subdeciduous & Dry	-1.0606061	-2.767539	0.6463267	0.2914375	
Evergreen & Dry	0.2121212	-1.494812	1.9190540	0.9498243	
Evergreen & Subdeciduous	1.2727273	-0.470918	3.0163725	0.1874172	
Adults					
Vegetation type	2	62.0	31.02	1.687	0.202
Residuals	31	570.2	18.39		
Tukey HSD test					
Subdeciduous & Dry	1.901515	-2.504547	6.307577	0.5442108	
Evergreen & Dry	3.265152	-1.140911	7.671214	0.1785533	
Evergreen & Subdeciduous	1.363636	-3.137191	5.864463	0.7384512	
Signif. codes: 0 ‘***’, 0.001 ‘**’, 0.01 ‘*’, 0.05 ‘.’, 0.1 ‘ ’ 1					

Table 5. Coefficients of three Generalized Lineal Models (GLM) analyses to social organization prediction by bioclimatic variables. One GLM per social aspect: Group size, subadults and adults (dependent variables), at the Yucatan jay pre-reproductive phase. The independent variables are the PCs of the bioclimatic principal component analysis that represent more of the 94% of the variance.

Group size				
Coefficients:	**Estimate**	**std.error**	**statistic**	**p value**
(Intercept)	-4.709907	2.489903	-1.891603	0.0618
PC1	-0.000291	0.000093	**-3.114935**	**0.0025***
PC2	0.000095	0.000138	0.690591	0.4916
PC3	0.000100	0.000074	1.359403	0.1775
PC4	-0.000187	0.000197	-0.953126	0.3431
Subadults				
(Intercept)	0.878475	1.219298	0.720476	0.473142
PC1	-0.000010	0.000046	-0.212880	0.831913
PC2	0.000037	0.000068	0.547396	0.585493
PC3	-0.000026	0.000036	-0.706515	0.481734
PC4	-0.000020	0.000096	-0.205566	0.837605
Adults				
(Intercept)	0.1221148	1.2187081	0.1002002	0.9204133
PC1	0.0000093	0.0000457	0.2037331	0.8390325
PC2	-0.0000363	0.0000675	-0.5379336	0.5919808
PC3	0.0000254	0.0000361	0.7042820	0.4831168
PC4	0.0000203	0.0000962	0.2110223	0.8333577
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				

Table 6. Regression results of nine Lineal Models (LM) analyses to social organization prediction by the three Colwell's (1974) indexes in rainfall occurrence (in 90 years). One LM per social aspects (Group size, subadults and adults) as the dependent variables, and rainfall index (predictability, constancy and contingency), as the independent variables at the Yucatan jay *pre-reproductive* phase.

Independent var.	*Dependent var.*								
	Group size			**Subadults**			**Adults**		
Predictability	-0.571 (6.908)			-4.802 (3.074)			4.231 (6.403)		
Constancy		-3.108 (7.841)			**-7.704**** (3.446)			4.596 (7.276)	
Contingecy			4.422 (10.708)			2.809 (4.824)			1.614 (9.957)
Const**ant**	7.534** (3.107)	8.273*** (2.548)	6.726*** (1.415)	4.201*** (1.383)	4.528*** (1.120)	1.713*** (0.638)	3.332 (2.880)	3.745 (2.364)	5.013*** (1.316)
Observations	93	93	93	93	93	93	93	93	93
R2	0.0001	0.002	0.002	0.026	**0.052**	0.004	0.005	0.004	0.0003
Adjusted R2	-0.011	-0.009	-0.009	0.015	0.042	-0.007	-0.006	-0.007	-0.011
Residual Std. Error (df = 91)	4.384	4.380	4.380	1.951	1.925	1.973	4.063	4.064	4.073
F Statistic (df = 1; 91)	0.007	0.157	0.171	2.440	**4.999****	0.399	0.437	0.399	0.026
Note: *p<0.1; **p<0.05; ***p<0.01									

Figure S1: Estimates of heterozygosity (ObsHet and ExpHet) and nucleotides diversity (Pi) in the Yucatan Jay with the American crow alignments (population maps with two CB2OGU and three CB3OGU represented OGUs), without alignments for run1 and run2 (R1POP and R2POP) and with the Zebra f nch alignments (ZFPOP).

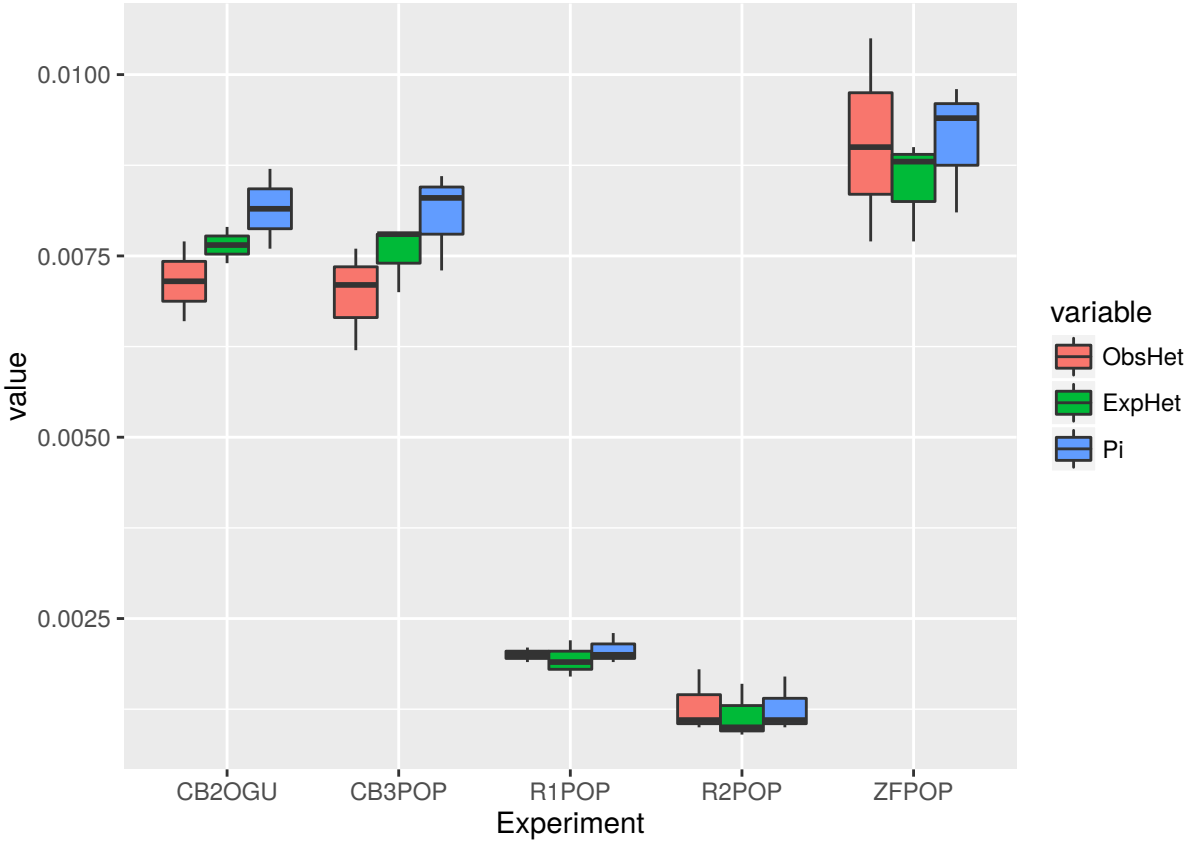


Figure S2: Standard errors of heterozygosity and nucleotide diversity (Pi) estimates in the Yucatan Jay with the American crow alignments (population maps with two CB2OGU and three CB3OGU represented OGUs), without alignments for run1 and run2 (R1POP and R2POP) and with the Zebra f nch alignments (ZFPOP).

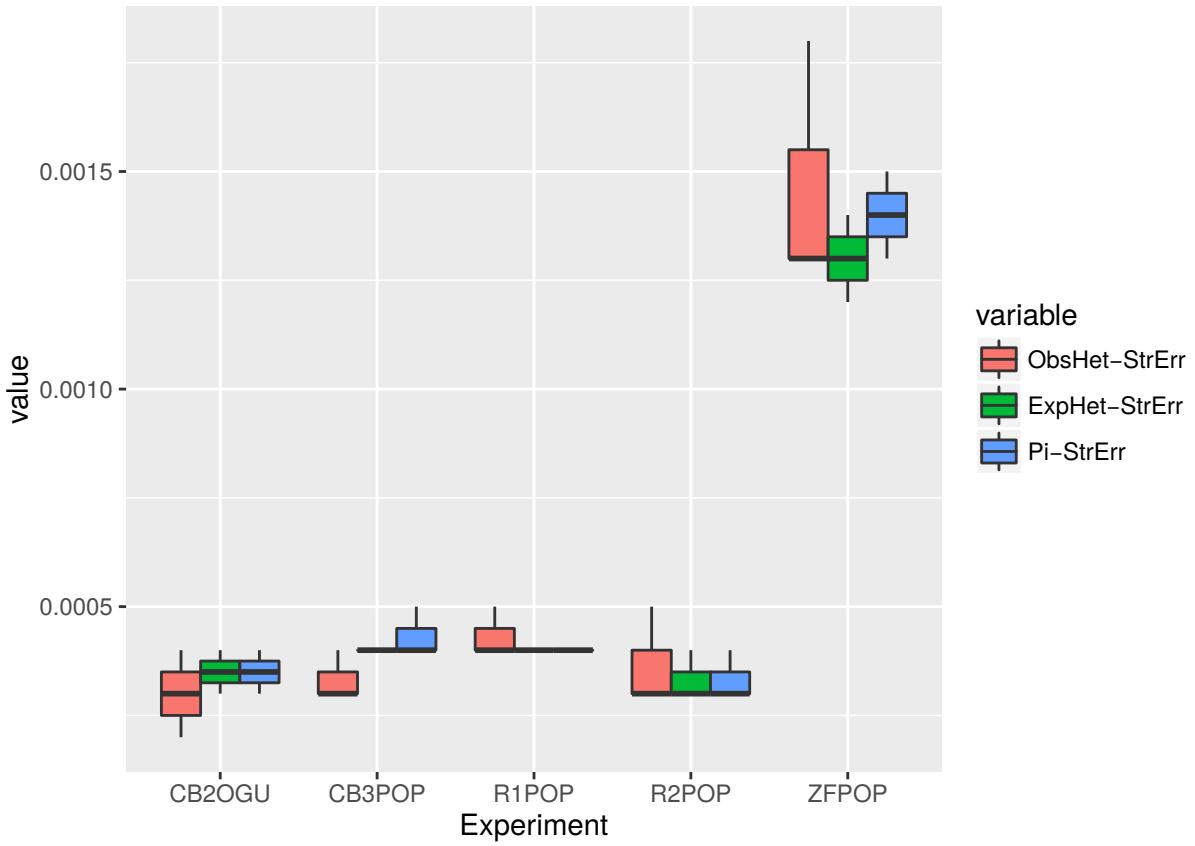


Figure S3: Variance of heterozygosity and nucleotide diversity (Pi) estimates in the Yucatan Jay with the American crow alignments (population maps with two CB2OGU and three CB3OGU represented OGUs), without alignments for run1 and run 2 (R1POP and R2POP) and with the Zebra f nch alignments (ZFPOP).

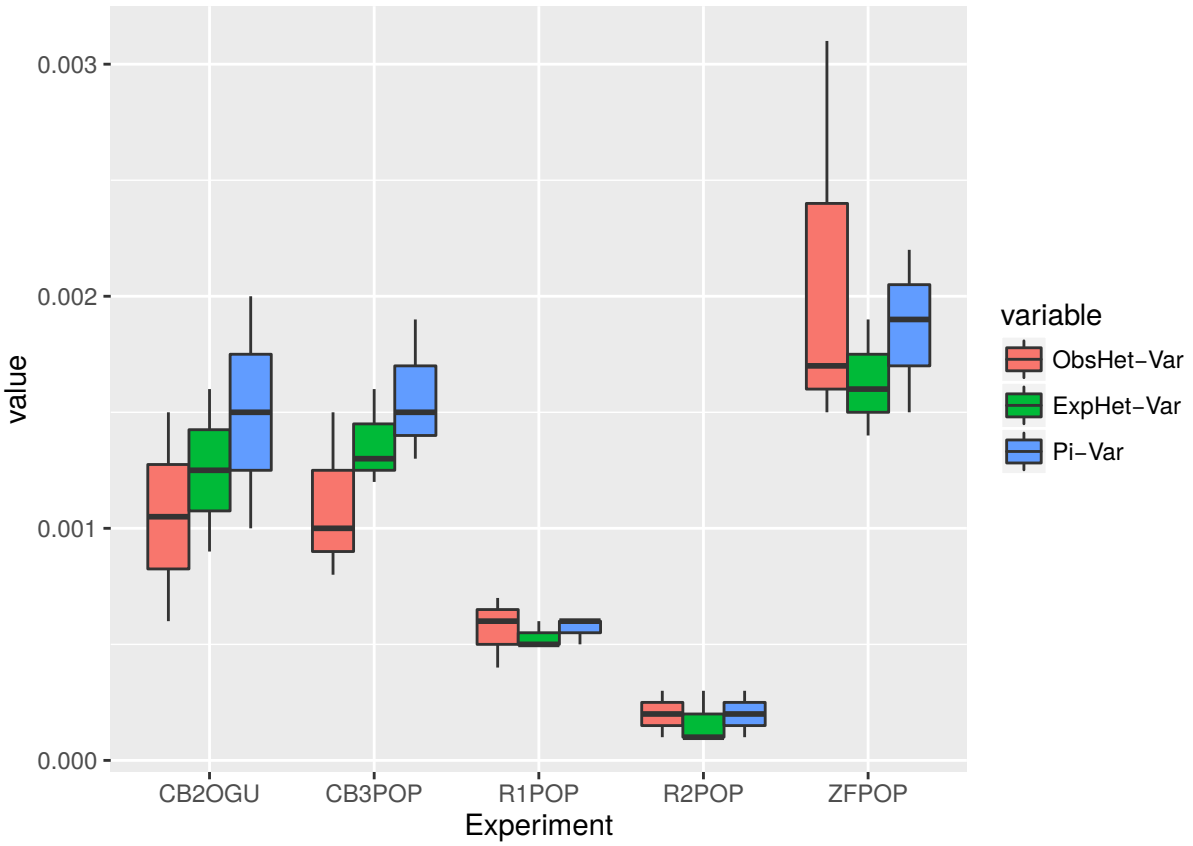


Figure S4: Estimates of f xation index (Fis) and standard errorsr in the Yucatan Jay with the American crow alignments (population maps with two CB2OGU and three CB3OGU represented OGUs), without alignments for run1 and run 2 (R1POP and R2POP) and with the Zebra f nch alignments (ZFPOP).

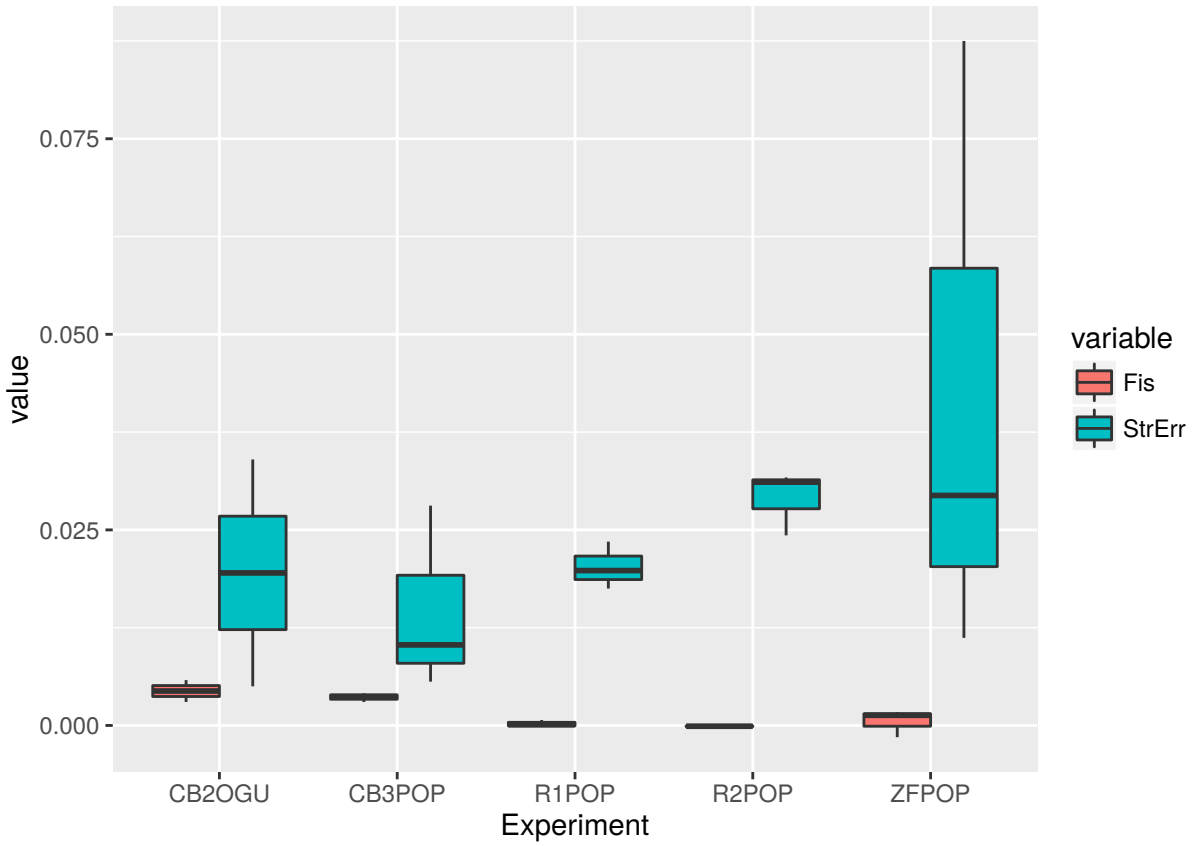


Figure S5: Major allele frequency in the Yucatan Jay with the American crow alignments (Cb) without close reference genome alignments for run1 and run 2 (R1 and R2) and with the Zebra f nch alignments (ZF).

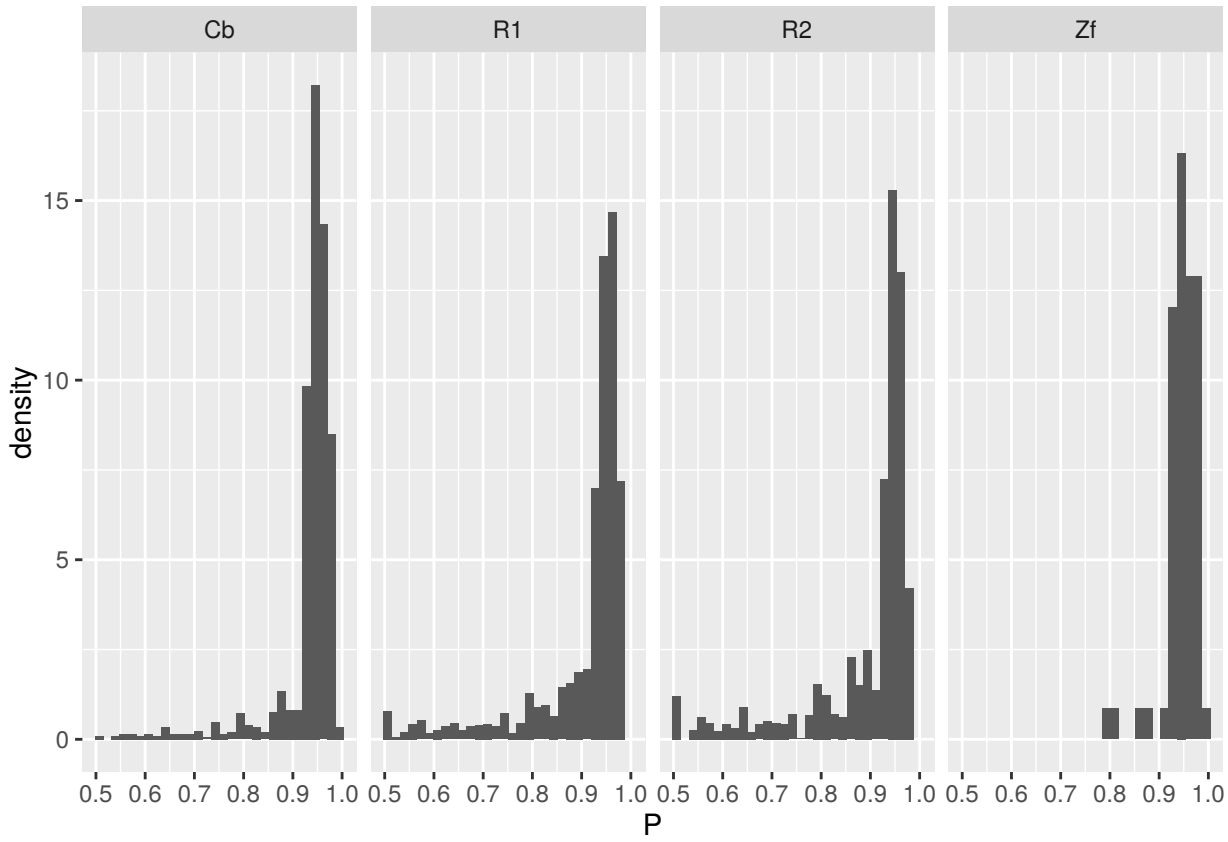


Figure S6: RAD sites, variant sites and polymorphic site obtained after SNP discovery analysis in the Yucatan Jay with the American crow alignments (population maps with two CB2OGU and three CB3OGU represented OGUs), without alignments for run1 and run 2 (R1POP and R2POP) and with the Zebra f nch alignments (ZFPOP).

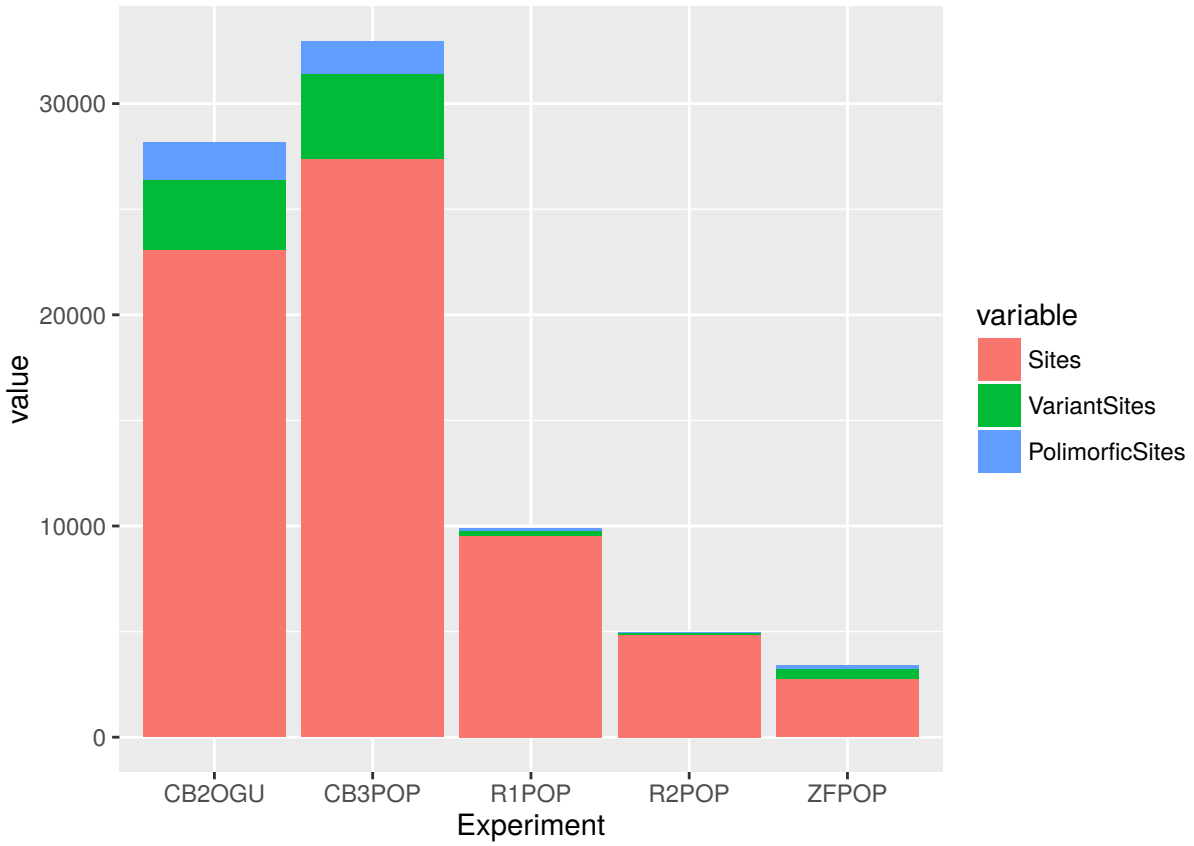

30000
20000
10000
0
value
CB2OGU
CB3POP
R1POP
R2POP
ZFPOP
Experiment
variable
Sites
VariantSites
PolimorficSites

Figure S7: Regression plot (LM) between the American crow scaf olds length on bp and the number of SNPs retained for the Yucatan jay with the American crow alignment as pseudo reference genome. Values are represented in logarithms.

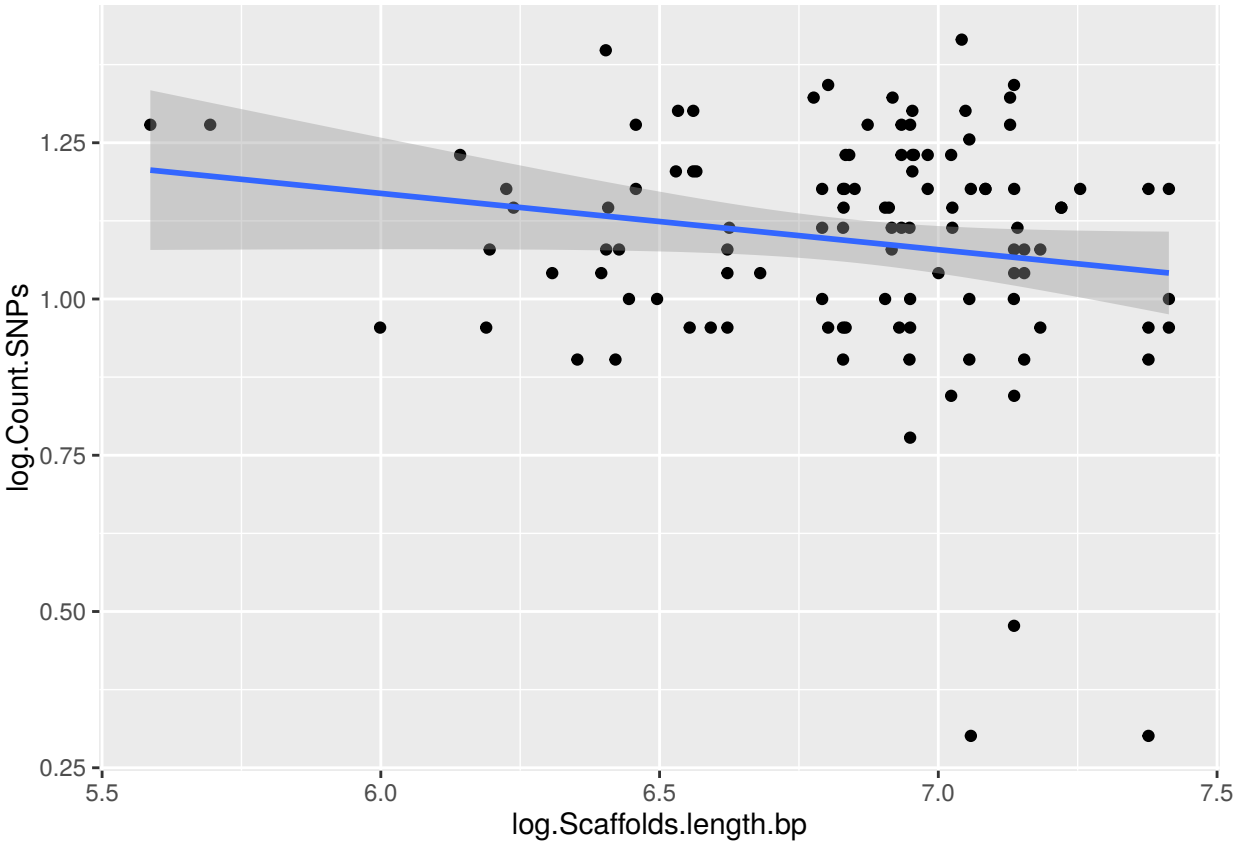


Figure S8: BayeScan 2.1 plot of 1649 polymorphic markers in the global enhanced genome scan analysis of 38 individuals from three Yucatan Jay populations. FST is plotted against the log10 of the posterior odds (PO) non outlier markers were identifying with this method.

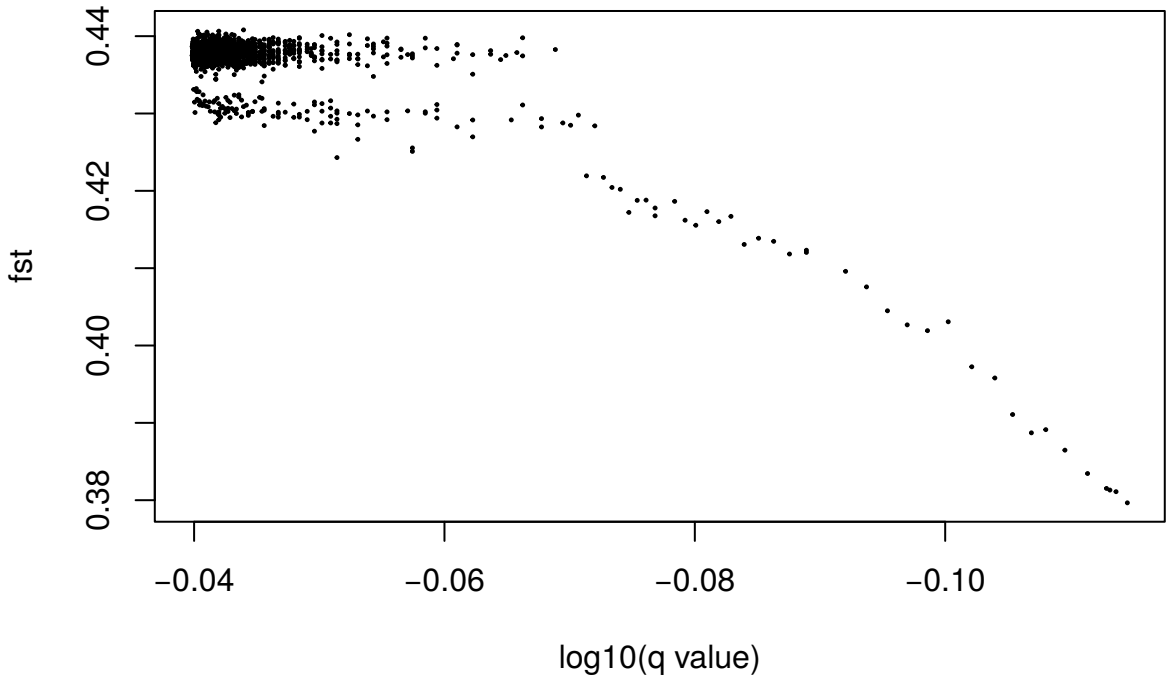


Figure S9: PCA plot on morphometric variables of the Yucatan jay. PCs that represent more than the 80% of variation. Groups represented at the three predominant OGUs; a (north), d (central) and g (south).

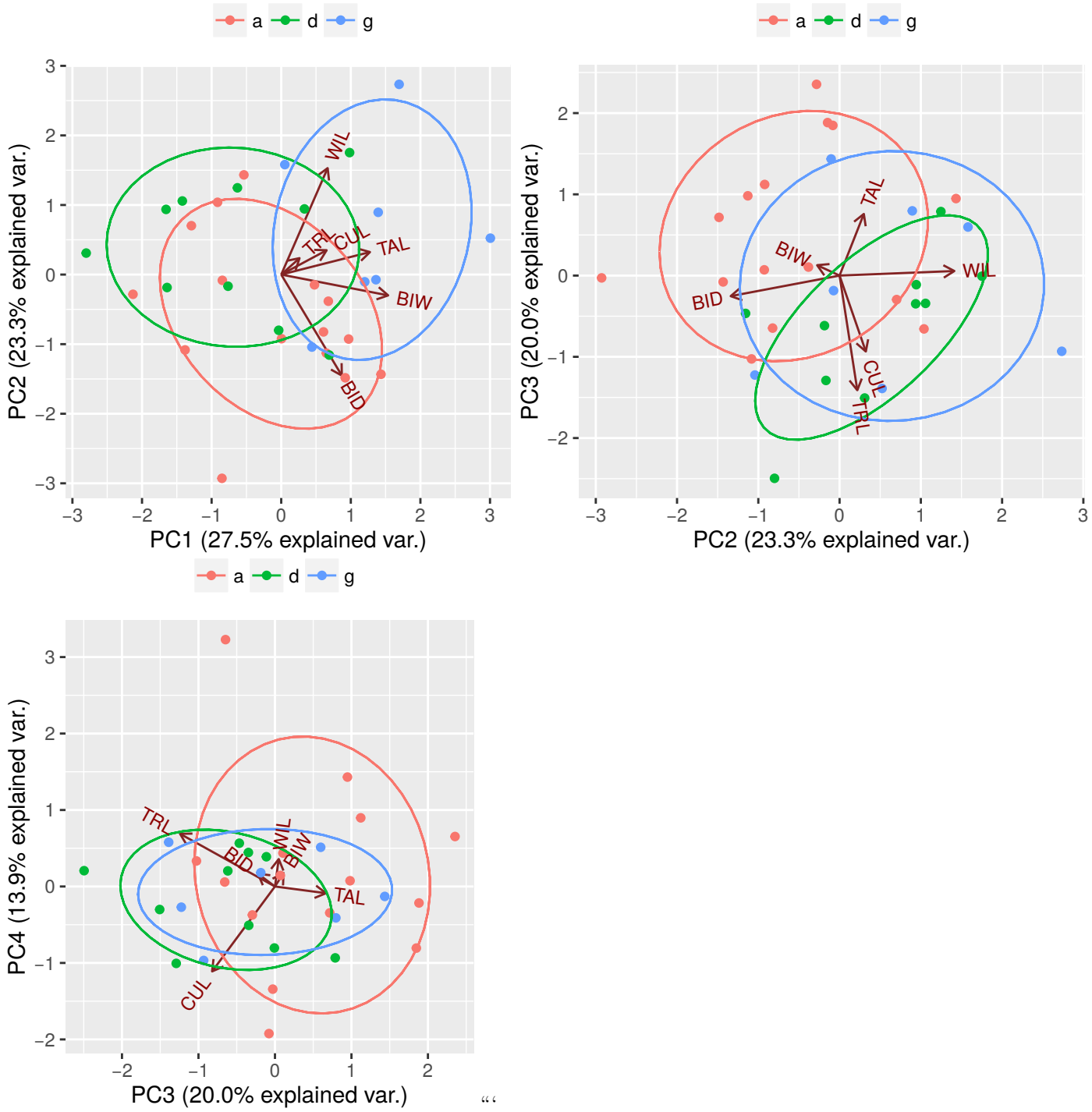
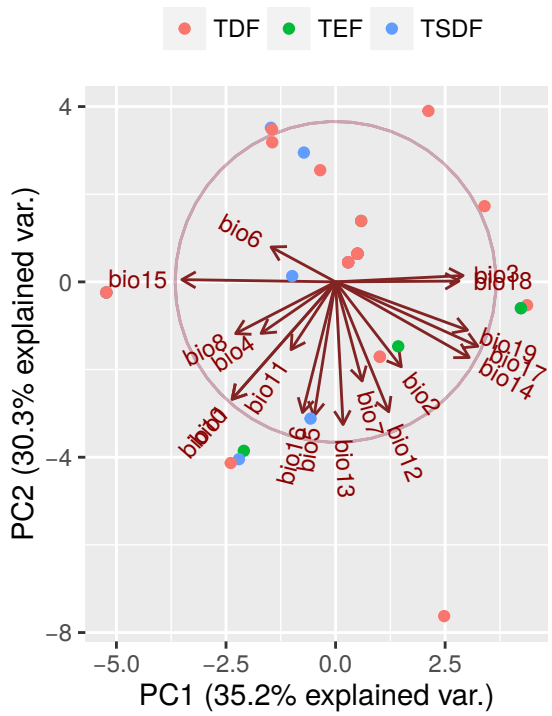
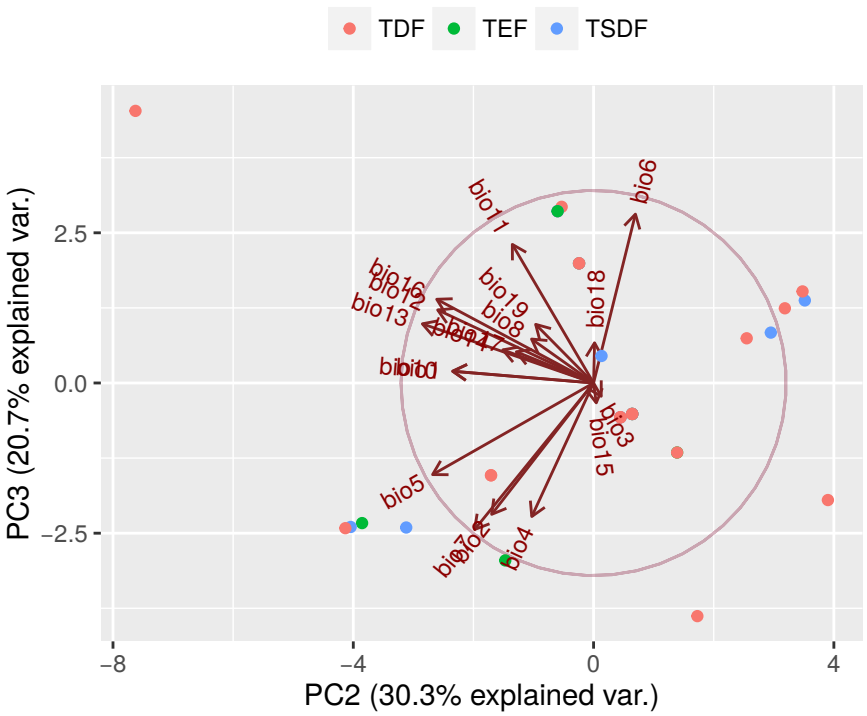


Figure S10: PCA plot on bioclimatic variables of the Yucatan peninsula. PCs that represent more than the 80% of variation. Groups represented at the three predominant types of vegetations, TDF=Tropical Dry Forest, TSDF=Tropical Subdeciduous Forest and TEF=Tropical Evergreen Forest.


TDF
TEF
TSDF
PC2 (30.3% explained var.)
PC1 (35.2% explained var.)
bio15
bio6
bio18
bio3
bio8
bio4
bio11
bio19
bio17
bio14
bio2
bio7
bio12
bio13
bio5
bio16
bio9
bio1


TDF
TEF
TSDF
PC3 (20.7% explained var.)
PC2 (30.3% explained var.)
bio11
bio6
bio18
bio19
bio8
bio13
bio3
bio15
bio5
bio4

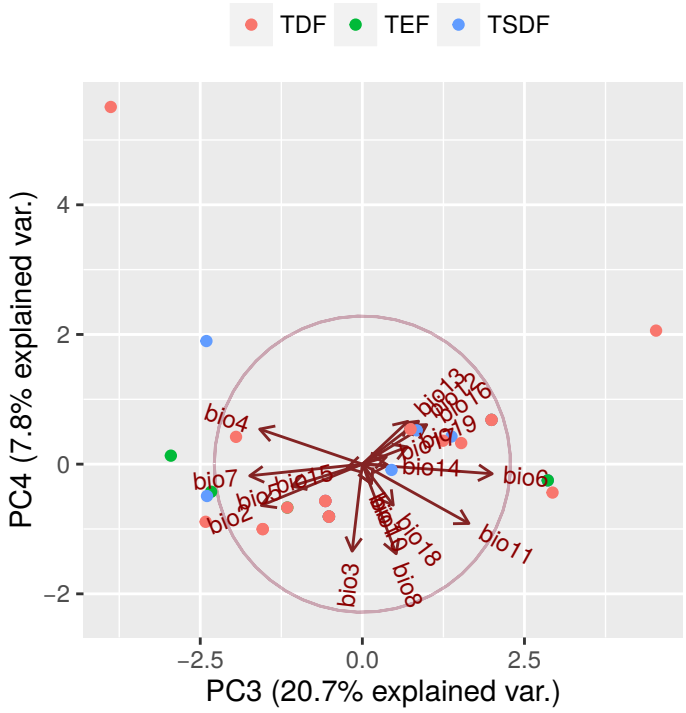

TDF
TEF
TSDF
PC4 (7.8% explained var.)
PC3 (20.7% explained var.)
bio4
bio7
bio14
bio6
bio11
bio18
bio8
bio3

Table S1: Outliers loci identified in LFMM associations analysis on phenotype and environmental variables at three latent factors (LF) in the fourth PCs that explained the variance. Candidate genes flanked the sequence after MegaBlasted and molecular/biological function known or hypothesized in birds.

Locus	Morphometric															
	LF1				LF2				LF3				BLAST genes[a]	BLASTed on birds sp.[b]	Scaffold/ Chr[c]	Product	Molecular and Biological function[d]
	PCA-Var LFMM log10(p-value)*																
	PC1	*PC2*	*PC3*	*PC4*	*PC1*	*PC2*	*PC3*	*PC4*	*PC1*	*PC2*	*PC3*	*PC4*					
733	5	5.5		5	5	5		5	5	5		5	LOC104692606 (PSCA) '5 / ARC '3	3	89 / 2	prostate stem cell antigen-like / activity-regulated cytoskeleton-associated	Prevents programmed cell death of Parasympathetic neurons (Hruska et al. 2009) / Actin binding, associated with the cell cortex of neuronal soma and dendrites. Enriched in postsynaptic density of dendritic spines. Required for consolidation of synaptic plasticity as well as formation of long-term memory (Velho et al. 2005).
12405				3.5									IGF1 5' / LOC104696496 3'	25	56 / 1A	Insulin-like growth factor 1 / tyrosine 3-monooxygenase-like	Bone mineralization involved in bone maturation. Response to heat, water homeostasis.
6238				3.5				3.5				3.5	SALL 5' / KIAA0319 3'	50	146 / 2	sal-like protein 3 / dyslexia-associated protein	RNA polymerase II core promoter proximal region sequence-specific DNA binding transcription factor activity involved in negative regulation of transcription-pituitary gland development, outer ear morphogenesis, gonad development / neuronal migration and negative regulation of dendrite development.
4239											4		SUCLA2 5' / HTR2A 3'	3	202 / 1	succinate-CoA ligase, ADP-forming, beta subunit / 5-hydroxytryptamine (serotonin) receptor 2A, G protein-coupled, transcript variant X1	Carbon metabolism / Serotonin receptor activity. Regulation of behavior, hormone secretion.
Locus	**Bioclimatic**																
2144			3.8				3				4		CCDC85C	7	1 / 5	coiled-coil domain containing 85C	Cerebral cortex development.
29229			3										MCTP1	3	22 / Z	multiple C2 domains, transmembrane 1, transcript factor variant X1	Calcium ion bandin.
4972			7.8		4		7		4.5		6		ITGA4 '5 / UBE2E3 '3	2	255 / 7	integrin, alpha 4 (antigen CD49D, alpha 4 subunit of VLA-4 receptor) / ubiquitin-conjugating enzyme E2 E3	Protein involved in the adherence of cells to other cells or to a matrix. Cell adhesion is mediated by cell surface proteins. Ubiquitin-like modifier conjugation pathway.
12405			4								3		IGF1 5' / LOC104696496 3'	25	56 / 1A	Insulin-like growth factor 1 / tyrosine 3-monooxygenase-like	bone mineralization involved in bone maturation. Response to heat, water homeostasis.
6116			4				3				3		ZNF521 '5 / SS18 '3	3	106 / 2	zinc finger protein 521, transcript variant X2 / synovial sarcoma translocation, transcript variant X3	Ligand-dependent nuclear receptor transcription coactivator activity / Metal ion and nucleic acid binding. Neuronal stem cell population maintenance.
17628			4										KLHL32 '5 / NDUFAF4 '3	2	14 / 3	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex assembly factor 4 / kelch-like family member 32, transcript variant X1	Mitochondrial respiratory chain complex I assembly / hormone-regulated proliferation-associated protein of 20 kDa.
7213			3										DAPK1	5	37 / Z	death-associated protein kinase 1	ATP binding and protein kinase activity. Universally important coenzyme and enzyme regulator.
7557			3										MALRD1	3	167 / 2	MAM LDL-receptor class A domain-containing protein 1	Cholesterol homeostasis, biosyntetic process.
1041					5				3.8				MPPED2 5' / DNAJC24 3'	14	281 / 5	metallophosphoesterase domain containing 2 / Hsp40 homolog, subfamily C, member 24	Hydrolase activity. Metabolic proces. / DnaJ-Hsp40 proteins are highly conserved and play crucial roles in protein translation, folding, unfolding, translocation, and degradation (Ahmad et al. 2011). Molecular mechanisms underlying time-of-day-dependent responses to light (Hatori et al. 2011)

*Variables that explain the principal components in morphometry: PC1=TAL+BIW, PC2=WIL+BID, PC3=TAL+TRL+CUL, PC4= TRL+CUL

*Variables that explain the principal components in bioclimatic: PC1=Bio15+Bio17, PC2=Bio13+Bio5, PC3=Bio11+Bio4+Bio7, PC4=Bio8+Bio3

[a]Features flanking this part of subject sequence on 5' and 3' on the American crow genome

[b]sequence BLASTed on bird species with 80-100% identity and e-value 1e-4 or below. The first two always are American crow and Hooded crow

[c]genes on American crow scaffolds / Zebra Finch chromosomes

[d]molecular and biological function known on Zebra Finch or Chicken, obtained on Uniprot, QuickGO EMBL-EBI and experimental results from literature.

Table S2: Morphometric and bioclimatic principal component analysis results; standard deviations, rotations (or loadings) for each variables and scores of the principal component selected for the association analysis, for each individuals samples of the Yucatan jay.

MORPHOMETRIC ANALYSIS

Standard deviations:

	PC1	*PC2*	*PC3*	*PC4*	*PC5*
	1.2846495	*1.1824631*	*1.0949845*	*0.9148635*	*0.7627271*

Rotation or loadings:

WIL	*0.2796955*	*0.6969031*	*0.0298345*	*0.25980471*	*0.21568451*
TAL	*0.5349222*	*0.1473539*	*0.40415099*	*-0.06374415*	*-0.70435739*
TRL	*0.1104202*	*0.107672*	*-0.75170323*	*0.49926204*	*-0.30789987*
CUL	*0.2735244*	*0.1593233*	*-0.49786229*	*-0.80513959*	*0.01407468*
BIW	*0.6444368*	*-0.1362726*	*0.06813956*	*0.12803709*	*0.593803*
BID	*0.3651324*	*-0.6611093*	*-0.13492323*	*0.12055024*	*-0.09878471*

COMPONENT-SCORES

Yucatan jay samples, ID order and locality name

	PC1	*PC2*	*PC3*	*PC4*	*LOC*
1	*-1.3814244519*	*-1.0829046377*	*-1.0260089474*	*0.3337651482*	*"XCUCLIN"*
2	*-0.9143850061*	*1.0387730934*	*-0.6565806376*	*0.057924307*	*"XCUCLIN"*
3	*-0.5359475733*	*1.4329146131*	*0.9478877177*	*1.4307134524*	*"DZILAM"*
4	*-2.1296913924*	*-0.2833166711*	*2.3541660898*	*0.6532108487*	*"MARAZUL"*
5	*0.0045644053*	*-0.9216444868*	*1.1215771859*	*0.8971522041*	*"XCUCLIN"*
6	*0.6772932097*	*-0.3829284289*	*0.1046781475*	*0.4368212568*	*"XCUCLIN"*
7	*1.4344094864*	*-1.4329138225*	*-0.0781172909*	*-1.9236988054*	*"MARAZUL"*
8	*0.4780084671*	*-0.1472376244*	*1.8831518779*	*-0.2159772972*	*"DZILAM"*
9	*0.6487091208*	*-1.1290295119*	*0.9819752721*	*0.0748587096*	*"XCUCLIN"*

10	0.9203183342	-1.4834345213	0.7165388508	-0.3450121068	"MARAZUL"
11	-0.8512250203	-2.9281826536	-0.02850358	-1.3424884508	"MARAZUL"
12	0.9690594356	-0.9265161723	0.0707410083	0.1441143777	"XCUCLIN"
13	-0.8457194262	-0.082796627	1.8483235809	-0.8057150619	"MARAZUL"
14	-1.2905695234	0.7023775918	-0.2952979215	-0.372458364	"XCUCLIN"
15	-1.4203654073	1.0578633414	-0.3424996517	-0.5081130432	"TZTIGRE"
16	0.6900236083	-1.1566433027	-0.4659610481	0.5658710258	"ECHENK"
17	-0.6289952109	1.2471232939	0.7880021966	-0.9337109431	"PCHENK"
18	-1.6544401223	0.9367193718	-0.3471821402	0.4444870625	"ECHENK"
19	-0.0360734324	-0.800559094	-2.4955677163	0.2063843429	"TZNOHBEC"
20	-1.6401253346	-0.1858792505	-0.6162211071	0.2040266396	"ECHENK"
21	0.3340434692	0.9438631997	-0.1121449921	0.3887120797	"LAGART"
22	0.6077863152	-0.8237299041	-0.6464439916	3.2283216858	"TZNOHBEC"
23	0.9826036959	1.7528810996	-0.0076569928	-0.8044218197	"PCHENK"
24	-0.7637022119	-0.1673391513	-1.2908485374	-1.0057892055	"ECHENK"
25	-2.8020262801	0.3090372287	-1.5071202855	-0.3012172646	"PCHENK"
26	3.0054580359	0.5231657629	-1.3893774739	0.5786146534	"ESCAR"
27	0.0517208158	1.5806737617	0.5977757369	0.5125726401	"SIANK"
28	1.3936848816	0.8950168123	0.7964742865	-0.4106400716	"SIANK"
29	1.69438028	2.7340379179	-0.9318798663	-0.967440792	"VILLA"
30	0.4410939025	-1.0417830637	-1.2241951997	-0.2706930231	"XPUJIL"
31	1.3612049882	-0.0737149236	-0.1852649041	0.1800134682	"SIANK"
32	1.2003279414	-0.1038932407	1.4355803334	-0.1301876534	"SIANK"
	NA	NA	NA	NA	"CONKAL"
	NA	NA	NA	NA	"CUXTALUMA"
	NA	NA	NA	NA	"CUXTALUMA"

NA	*NA*	*NA*	*NA*	*"CONKAL"*
NA	*NA*	*NA*	*NA*	*"CUXTALUMA"*
NA	*NA*	*NA*	*NA*	*"XMATKUIL"*

BIOCLIMATIC ANALYSIS

Standard deviations:

PC1	*PC2*	*PC3*	*PC4*	*PC5*
2.52E+000	*2.33E+000*	*1.93E+000*	*1.18E+000*	*8.22E-001*

Rotation or loadings:

bio1	*-0.25608291*	*-0.313475253*	*0.03158918*	*-0.110708771*	*-0.0003410048*
bio10	*-0.25608291*	*-0.313475253*	*0.03158918*	*-0.110708771*	*-0.0003410048*
bio11	*-0.11011905*	*-0.180773809*	*0.37248474*	*-0.337992815*	*-0.3071978157*
bio12	*0.13168963*	*-0.346849223*	*0.19644009*	*0.244936444*	*-0.0151210291*
bio13	*0.01856899*	*-0.380961791*	*0.15901968*	*0.243565231*	*0.091241127*
bio14	*0.33068641*	*-0.201938503*	*0.08904193*	*-0.005673468*	*-0.2388597491*
bio15	*-0.38054018*	*0.005990672*	*-0.05340622*	*-0.021529529*	*0.1274102006*
bio16	*-0.08173552*	*-0.348948461*	*0.22501599*	*0.225181706*	*0.0721736114*
bio17	*0.35224887*	*-0.17187661*	*0.08385368*	*0.042309928*	*-0.0363781487*
bio18	*0.3055316*	*0.002139391*	*0.10797531*	*-0.233512947*	*0.6028201591*
bio19	*0.32658876*	*-0.128870463*	*0.15757451*	*0.098349624*	*0.3551292438*
bio2	*0.16268861*	*-0.226742776*	*-0.353068*	*-0.235604431*	*-0.0809146188*
bio3	*0.31582152*	*0.016918978*	*-0.03573889*	*-0.495689093*	*-0.0384201463*
bio4	*-0.18435835*	*-0.137471031*	*-0.35892739*	*0.199710406*	*0.419053176*
bio5	*-0.05335142*	*-0.358149514*	*-0.24625296*	*-0.125011577*	*-0.1498736951*
bio6	*-0.15964953*	*0.093117511*	*0.45388393*	*-0.054881331*	*0.0262455466*
bio7	*0.06569499*	*-0.264641935*	*-0.39379784*	*-0.066329109*	*-0.0715550901*

bio8	-0.24748103	-0.137996927	0.11815092	-0.510485797	0.3403631681

COMPONENT-SCORES

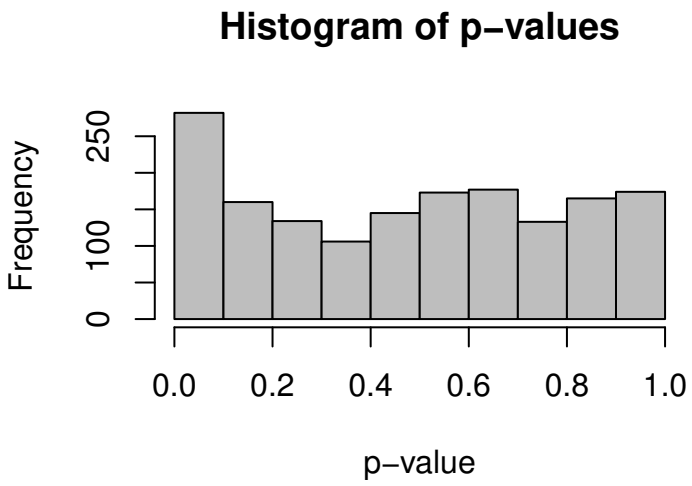
Yucatan jay samples, ID order and locality name

	PC1	PC2	PC3	PC4	LOC
1	-2.0924098281	-3.8536134838	-2.3322396746	-0.4255430513	"PCHENK"
2	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"XCUCLIN"
3	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"XCUCLIN"
4	1.4298819127	-1.4697696769	-2.9536225979	0.1309529164	"TZTIGRE"
5	0.5833247437	1.3902969341	-1.1576738355	-0.6693192834	"DZILAM"
6	-5.2294829188	-0.2418197432	1.992119994	0.6827642024	"ECHENK"
7	-0.570290666	-3.1187913538	-2.4054821414	1.8986551238	"MARAZUL"
8	0.2878884585	0.4469417465	-0.5707890875	-0.5680508094	"XCUCLIN"
9	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"CONKAL"
10	-0.7230439621	2.9504558301	0.8384110045	0.522013365	"CUXTALUMA"
11	-1.4750394799	3.5167174245	1.374401841	0.4267615987	"XMATKUIL"
12	-0.9894803941	0.1322559387	0.4500076428	-0.0887956375	"PCHENK"
13	-2.2038758025	-4.0440429033	-2.3964829928	-0.491014501	"XCUCLIN"
14	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"MARAZUL"
15	0.2878884585	0.4469417465	-0.5707890875	-0.5680508094	"ECHENK"
16	-5.2294829188	-0.2418197432	1.992119994	0.6827642024	"DZILAM"
17	0.5833247437	1.3902969341	-1.1576738355	-0.6693192834	"XCUCLIN"
18	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"MARAZUL"
19	4.3688354368	-0.5315291877	2.9327587593	-0.4382138695	"MARAZUL"
20	0.2878884585	0.4469417465	-0.5707890875	-0.5680508094	"CUXTALUMA"
21	4.2295109315	-0.5985577699	2.8598897188	-0.2501170479	"TZNOHBEC"

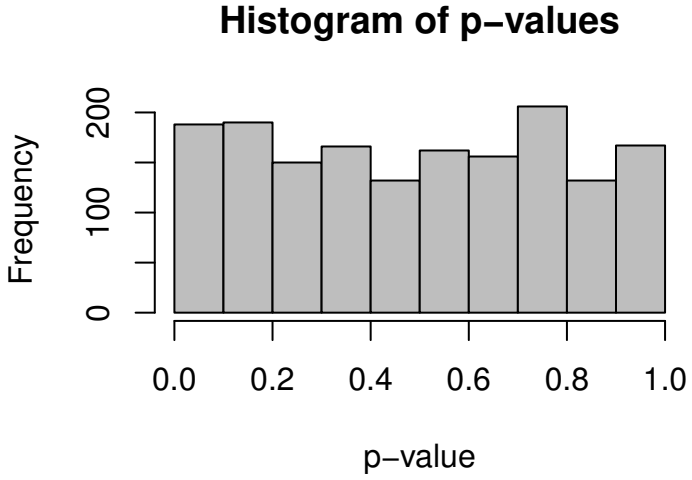
22	0.2878884585	0.4469417465	-0.5707890875	-0.5680508094	"CONKAL"
23	-1.4505879013	3.4782745106	1.5244906242	0.3252049065	"CUXTALUMA"
24	1.0098033947	-1.7070710827	-1.5365171464	-1.0017475825	"ECHENK"
25	-0.3507338872	2.5487884	0.7439066236	0.5384249241	"LAGART"
26	-1.44411754	3.1842749195	1.2432440797	0.3613884569	"XCUCLIN"
27	-5.2294829188	-0.2418197432	1.992119994	0.6827642024	"TZNOHBEC"
28	2.1183948883	3.9006538157	-1.9485614507	0.4211583831	"MARAZUL"
29	2.477647312	-7.6253518581	4.5296438373	2.0594746129	"PCHENK"
30	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"XCUCLIN"
31	1.0098033947	-1.7070710827	-1.5365171464	-1.0017475825	"ECHENK"
32	3.3990665084	1.7276682884	-3.8805504009	5.5090027233	"ESCAR"
33	0.2878884585	0.4469417465	-0.5707890875	-0.5680508094	"SIANK"
34	-2.3923896965	-4.1317578923	-2.4171514958	-0.8890249582	"SIANK"
35	0.5002633444	0.6425084394	-0.515513627	-0.8083946971	"VILLA"
36	4.2295109315	-0.5985577699	2.8598897188	-0.2501170479	"XPUJIL"
37	-5.2294829188	-0.2418197432	1.992119994	0.6827642024	"SIANK"
38	4.2295109315	-0.5985577699	2.8598897188	-0.2501170479	"SIANK"

Figure S11: LFMM p-value histogram plots to evaluate model runs acuracy for bioclimatic associations at each LF and PCs were outliers SNPs were present; a) LF1 at PC3; b) LF2 at PC1 c)LF2 at PC3; d) LF3 at PC1; e)LF3 at PC3.

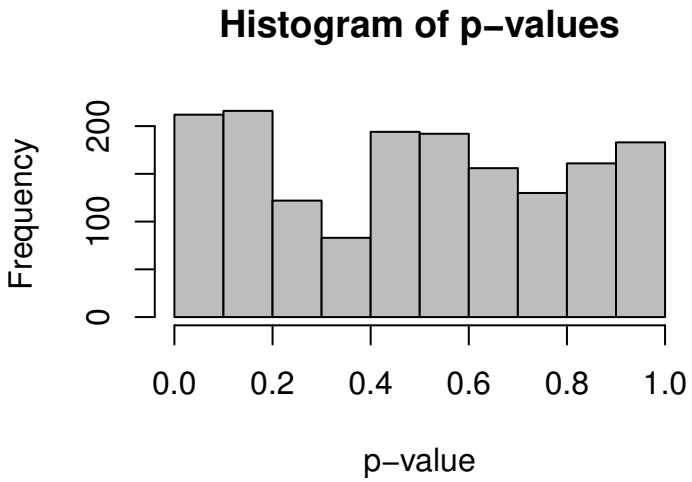
a)



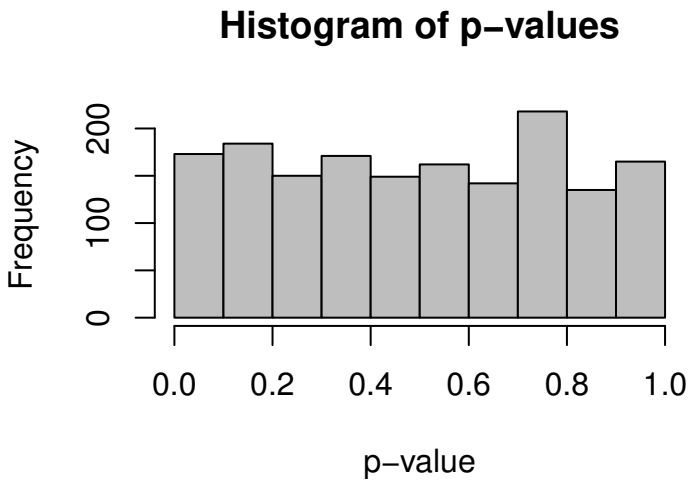
b)



c)


Histogram of p−values
Frequency
0
100
200
0.0
0.2
0.4
0.6
0.8
1.0
p−value

d)


Histogram of p−values
Frequency
0
100
200
0.0
0.2
0.4
0.6
0.8
1.0
p−value

e)

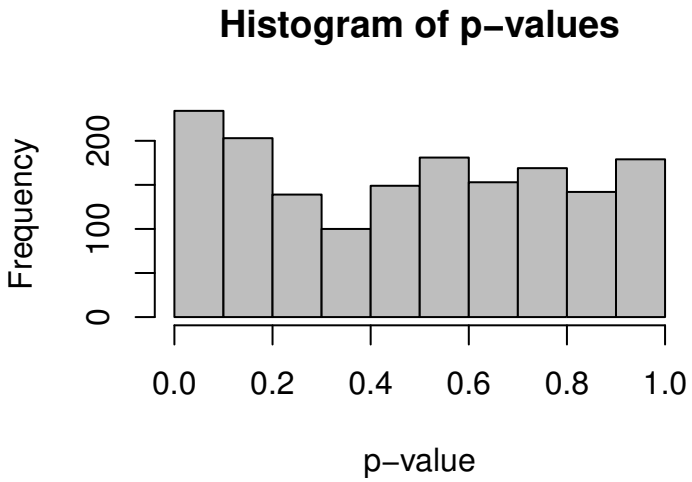
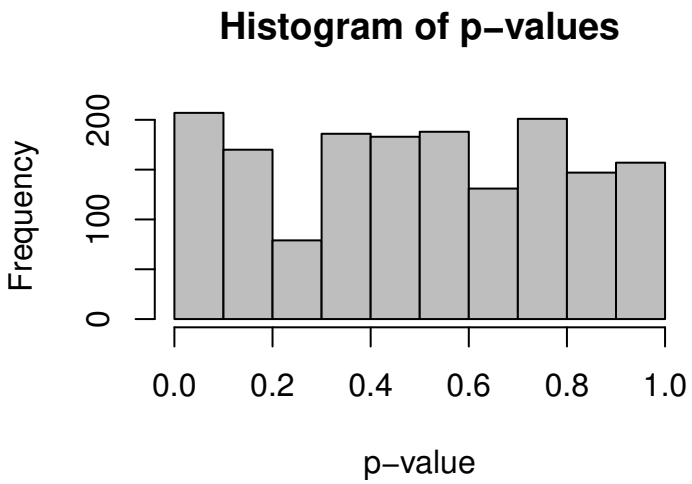
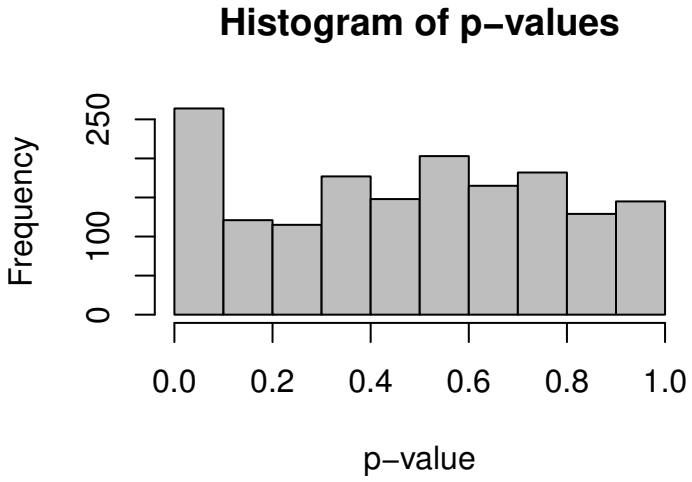

Histogram of p−values
Frequency
0
100
200
0.0
0.2
0.4
0.6
0.8
1.0
p−value

Figure S12: LFMM histograms of p-values to evaluate model runs acuracy for morphological associations analysis at LF1, LF2 and LF3 for PCs were outliers SNPs present; a) LF1 at PC1; b) LF1 at PC2; c) LF1 at PC4; d)LF2 at PC1; e)LF2 at PC2; f)LF2 at PC4; g)LF3 at PC1; h)LF3 at PC2; i)LF3 at PC4.

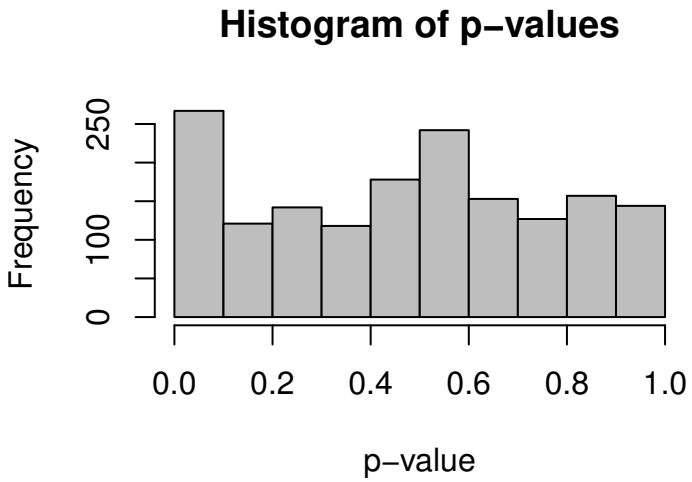
a)



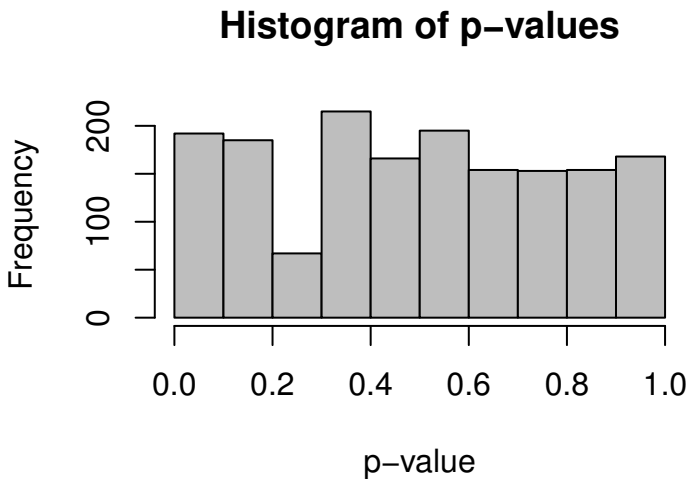
b)



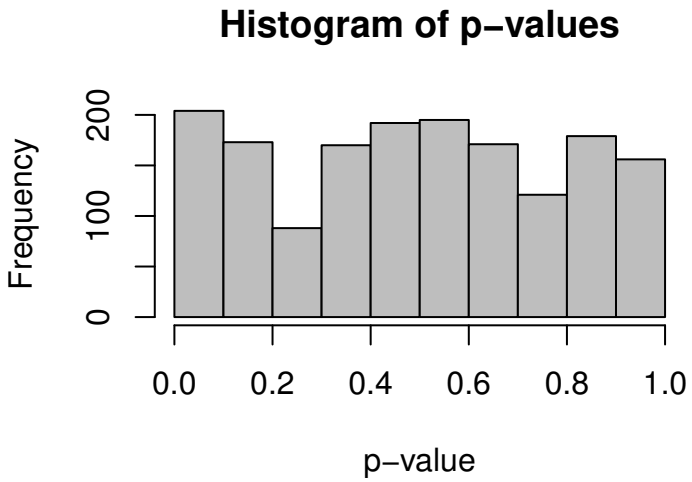
c)


Histogram of p−values
Frequency
0
100
250
0.0
0.2
0.4
0.6
0.8
1.0
p−value

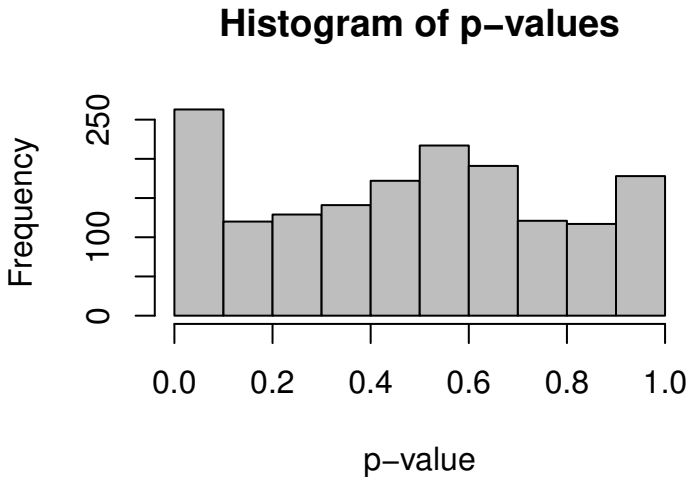
d)


Histogram of p−values
Frequency
0
100
200
0.0
0.2
0.4
0.6
0.8
1.0
p−value

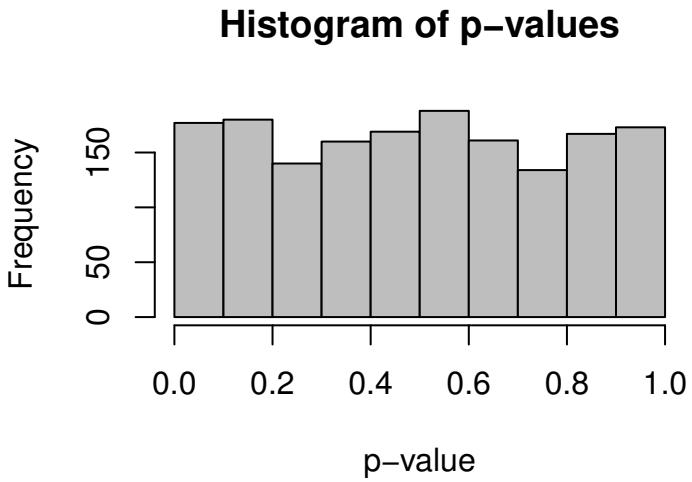
e)


Histogram of p−values
Frequency
0
100
200
0.0
0.2
0.4
0.6
0.8
1.0
p−value

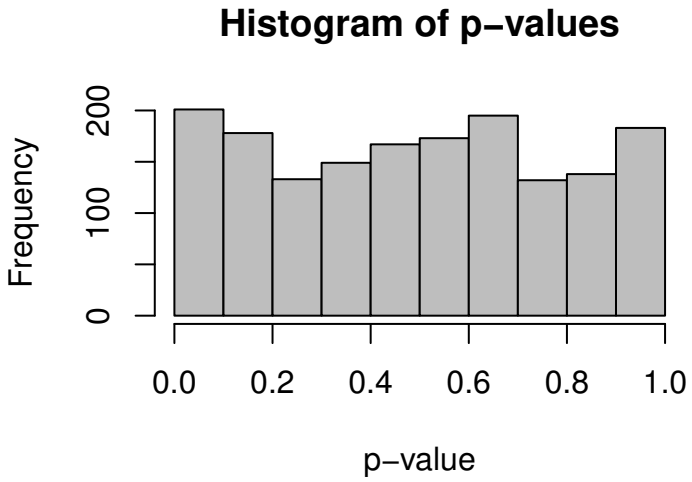
f)


Histogram of p−values
Frequency
0
100
250
0.0
0.2
0.4
0.6
0.8
1.0
p−value

g)


Histogram of p−values
Frequency
0
50
150
0.0
0.2
0.4
0.6
0.8
1.0
p−value

h)


Histogram of p−values
Frequency
0
100
200
0.0
0.2
0.4
0.6
0.8
1.0
p−value

i)

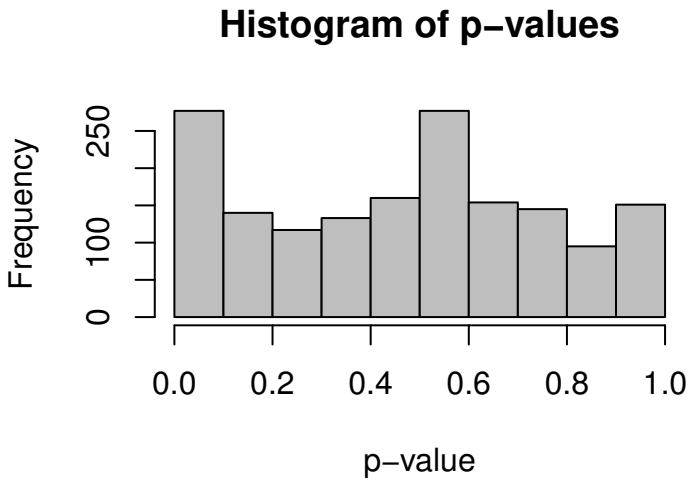
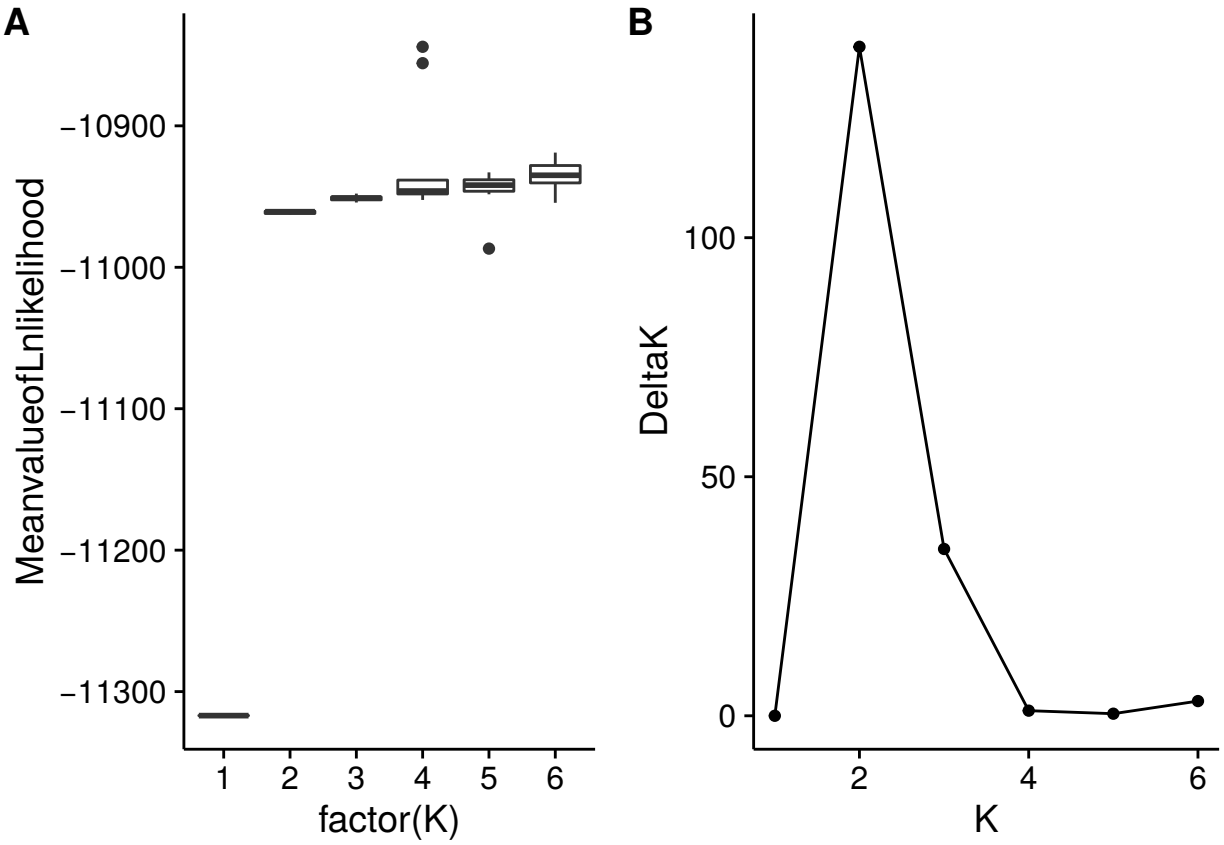

Histogram of p−values
Frequency
0
100
250
0.0
0.2
0.4
0.6
0.8
1.0
p−value

Figure S13: Structure plot an optimization of K=3 from STRUCTURE admixture analysis. a) Mean value of likelihood(ln) for each K value; b) Delta K for each K value from the harvester analysis to optimize K; c) Structure plot with ancestry proportion as Q value for each individuals ordered by gradiente, left side represent the north region and the dry tropical forest, the central part the subdecidious tropical forest and the right side the south region the evergreen tropical forest.



C