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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 Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 14 de septiembre de 2015, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **RUIZ SÁNCHEZ ANGELINA** con número de cuenta **512012775** con la tesis titulada: **"Ecología invernal del ave migratoria *Cardellina pusilla* en el bosque mesófilo de montaña del centro de Veracruz"**, realizada bajo la dirección de la **DRA. KATHERINE RENTON:**

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ÍNDICE

RESUMEN 1

ABSTRACT 3

INTRODUCCIÓN GENERAL 5

CAPÍTULO I
Ecological niche variation in the Wilson's Warbler *Cardellina pusilla* complex.......... 10
Abstract.......... 10
Introduction.......... 10
Methods.......... 11
Database.......... 11
Ecological niche modelling.......... 12
Niche similarity.......... 12
Interprediction approach.......... 13
Null model approach.......... 13
Ecological distance approach.......... 13
Results.......... 14
Interprediction.......... 14
Null model of similarity.......... 14
Ecological distance test.......... 16
Discussion.......... 16
Acknowledgments.......... 19
References.......... 19

CAPÍTULO II
Winter habitat disturbance influences density and territory size of a Neotropical migratoy warbler.......... 22
Abstract.......... 23
Introduction.......... 24
Methods.......... 26
Study area.......... 26
Forest structure.......... 26
Bird density.......... 27
Body condition.......... 27
Territory size.......... 27
Statistical analysis.......... 28
Results.......... 29
Habitat variation in forest structure 29
Variation in bird density.......... 29
Variation in territory size.......... 30
Body condition.......... 30

Discussion.......... 31
Acknowledgments.......... 31
References.......... 31

CAPÍTULO III
A two-way street: carry over effects of summer body condition on winter territory selection of a neotropical migratoy warbler 46
Abstract.......... 47
Introduction.......... 49
Methods.......... 51
Study area.......... 51
Bird capture and banding.......... 51
Body condition.......... 52
Feather coloration 52
Feather structure 53
Winter territory size.......... 54
Vegetation structure 55
Arthropod abundance 55
Statistical analysis.......... 56
Results.......... 57
Summer body condition and winter territory traits.......... 57
Relationships among winter territory traits.......... 58
Discussion.......... 59
References.......... 65

DISCUSIÓN GENERAL 80

RESUMEN

Las aves migratorias neotropicales enfrentan en la actualidad declines de poblaciones atribuidos principalmente a la modificación y pérdida de hábitat en los sitios donde invernan Sin embargo, se conoce poco de su ecología y de los factores que influencian sus oportunidades de éxito en invierno. Se estudió al Chipe corona negra (*Cardellina pusilla*), un ave migratoria neotropical, para evaluar aspectos de su ecología invernal a tres escalas: 1) continental, basado en características climáticas a lo largo de su distribución geográfica; 2) local, evaluando la influencia de la perturbación del hábitat por sitios e 3) individual, considerando la estructura de la vegetación y la abundancia del alimento de cada territorio.

En el primer capítulo se evalúa si los dos grupos genéticos y geográficos de *C. pusilla* tienen nichos ecológicos distintos. Se realizaron modelos de nicho con coberturas de temperatura y precipitación y se calcularon porcentajes de interpredictibilidad de los nichos de ambos grupos. Para determinar si los nichos son distintos, se realizó una prueba de similitud que compara las autopredicciones y pseudoréplicas de cada grupo y se compararon las distancias ecológicas al interior de los grupos contra la distancia ecológica entre grupos, con la ecuación de Gower. Los resultados indicaron que el nicho ecológico del grupo del Este es climáticamente más restringido que el nicho del Oeste. Las distancias ecológicas entre grupos indican diferenciación, a pesar de que existe traslape de las condiciones de nicho de ambos grupos. Por lo tanto se apoya la hipótesis de que *C. pusilla* es un complejo conformado por dos especies crípticas.

En el segundo capítulo se determinan los efectos de la perturbación del hábitat sobre la ecología invernal de *C. pusilla*. Se evaluó la densidad, el tamaño de territorio y la condición física de las aves en tres fragmentos de bosque mesófilo con distinto grado de perturbación. La densidad se estimó mediante puntos de conteo de radio variable. Se capturaron 74 individuos en tres temporadas invernales (2011-2014) para obtener su condición física (peso/ala) y se hicieron re-avistamientos y

seguimiento de los individuos marcados para definir el tamaño de territorio. El estudio reveló que en el bosque conservado la especie alcanza mayor densidad, los territorios son de menor tamaño y la condición física y el tamaño de territorio son estables entre años. Lo que indica que el bosque mesófilo conservado es un hábitat de mayor calidad para *C. pusilla*.

En el tercer capítulo se evaluó si existe relación entre la condición física de verano de las aves con la estructura de la vegetación, la abundancia del alimento y el tamaño del territorio invernal y a su vez, si estas variables tienen relación con la condición física invernal de las aves. Se marcaron 68 individuos territoriales durante el invierno (2011-2014) para obtener tres indicadores de la condición física de verano, de las plumas mudadas en verano: i) coloración amarilla de la pluma (dada por carotenoides), ii) estructura macroscópica (longitud y grosor de la pluma y ancho del ápice) y iii) estructura microscópica (longitud de las barbas y longitud y ancho de las bárbulas). El tamaño de territorio se obtuvo del re-avistamiento de aves marcadas. La estructura de la vegetación incluyó estimaciomes de área basal leñosa, abundancia de árboles y arbustos y altura de árboles y arbustos. La abundancia de artrópodos, presas de *C. pusilla*, se estimó con redes de barrido. El estudio mostró un efecto de la microestructura de la pluma sobre la calidad de hábitat donde se establecen los territorios invernales. Los individuos cuyas plumas tenían las bárbulas más largas establecieron territorios con alta abundancia de arbustos. Asimismo, la abundancia de arbustos y de árboles, presentó una relación positiva con la abundancia de alimento y negativa con el tamaño de territorio. Esto sugiere que los individuos de *C. pusilla* con mejor condición de verano establecen territorios en la vegetación leñosa conservada, que tiene más mayor abundancia de alimento, permitiéndoles mantener territorios pequeños con implicaciones potenciales en su adecuación. El estudio enfatizan la importancia de la conservación de bosques conservados como hábitat de alta calidad para las aves y resalta la influencia que tiene la condición física de las aves en verano sobre las oportunidades de las aves migratorias.

ABSTRACT

Neotropical migratory birds currently face population declines principally attributed to habitat loss and modification in the wintering grounds. However, little is known on the winter ecology of migratory birds, or the factors that influence avian opportunities during the winter. I studied the Wilson's Warbler (*Cardellina pusilla*), a Neotropical migratory bird, to evaluate aspects of the species' wintering ecology at three different levels: 1) continental, based on climatic characteristics over the species' entire geographical distribution, 2) local, evaluating the influence of habitat disturbance among sites, and 3) individual, considering vegetation structure and food abundance within each territory.

The first chapter evaluates whether the two genetic and geographic Wilson's Warbler groups have distinct ecological niches. I generated niche models with temperature and precipitation layers and calculated the degree of inter-prediction for both groups. To determine whether niches were distinct between the two groups, I used a similarity test that compares self-predictions and pseudo replicas of each group, and also used the Gower equation to compare ecological distances within each group vs that between groups. The results indicated that the ecological niche of the Eastern group is climatically more restricted that that of the Western group, and showed that even when there is some overlap in niche conditions for both groups, the ecological distances between groups indicate differentiation. Therefore, the study supports the hypothesis that the Wilsons Warbler complex is comprised of two cryptic species.

In the second chapter, I evaluated the effect of habitat disturbance on the wintering ecology of Wilsons Warbler. I determined the density, territory size, and body condition of birds in three cloud forest fragments with different degrees of disturbance. Density was estimated by unlimited radius point-counts. Body condition was obtained from 74 captured individuals (body mass/wing length), and individuals were resighted and followed to obtain territory size, over three winters

(2011-2014). The study revealed that in the conserved cloud forest the species reached its highest density, territories were smaller, and body condition and territory size were stable among years. This indicates that conserved cloud forest is a higher quality habitat for Wilsons Warbler.

In the third chapter, I evaluated the relationships of summer body condition of birds with vegetation structure, food abundance and the territory size in the wintering grounds. I also evaluated whether these variables were related to wintering body condition. I captured and marked 68 territorial individuals in the wintering ground (2011-2014), and used three indicators of summer body condition based on tail feathers molted in the breeding grounds: i) yellow feather coloration (created by carotenoids in the diet), ii) macroscopic feather structure (feather length and width, and apex width), and iii) microscopic structure (barb length, and barbule length and width). Territory size was obtained from resighting marked birds. Vegetation structure included estimation of woody basal area, tree and shrub abundance, and tree and shrub height. Abundance of arthropod prey consumed by Wilsons Warbler was estimated with sweep nets. The study demonstrated an effect of feather microstructure on the quality of habitat where birds established winter territories. Individuals with feathers with longer barbules established winter territories with high shrub abundance. Moreover shrub and tree abundance showed a positive relationship with food abundance, and a negative relationship with territory size. This suggests that Wilson’s Warblers with better summer body condition establish territories in conserved woody vegetation, that has higher food resource abundance, enabling them to maintain smaller winter territories, with potential long-term implications for fitness. The study emphasizes the importance of preserving conserved forests as a high quality habitat for birds, and highlights the influence of summer body condition on wintering opportunities for migratory birds.

INTRODUCCIÓN

En las últimas dos décadas se ha evidenciado en Norteamérica el decline de las poblaciones de aves migratorias neárticas neotropicales (Robbins et al. 1989, Askins et al. 1990, Ballard et al. 2003, Sauer et al. 2014), mientras que las poblaciones de aves residentes no muestran el mismo decremento (Rappole y McDonald 1994). La disminución de las poblaciones migratorias presenta una fuerte correlación con las tasas de pérdida del hábitat de invierno (Robbins et al. 1989; Askins et al. 1990); a su vez se ha observado una reducción en el número de individuos que regresan a sitios de reproducción después de la migración (Rappole y McDonald 1994), aunado a una disminución en la ocupación de sitios adecuados para la anidación (McShea et al. 1995). Por lo cual se ha sugerido que la dinámica poblacional de las aves migratorias está siendo afectada por procesos que ocurren en los sitios en donde pasan el invierno (Rappole y McDonald 1994).

El hábitat en los sitios de migración de invierno puede determinar la condición física, la supervivencia y la adecuación de las aves. En el caso de *Setophaga ruticilla* (Parulidae) los individuos que ocupan sitios de mayor calidad durante el invierno en Jamaica tienen mejor condición física y llegan primero a territorios de reproducción, que las que ocupan sitios subóptimos, elevando sus probabilidades de éxito reproductivo (Marra et al. 1998, Marra y Holmes 2001). Sin embargo, se conoce poco acerca del uso de hábitat de las aves migratorias durante su estancia en los trópicos, el cual varía ampliamente entre especies (Rappole y McDonald 1994, Marra et al. 1998, Brown y Long 2007).

Cabe destacar que se ha registrado mayor declive en las poblaciones de aves que utilizan zonas boscosas durante el invierno comparado con las poblaciones que habitan zonas de vegetación abierta (Robbins et al. 1989). México alberga grandes concentraciones de aves migratorias neotropicales; en particular los bosques de la vertiente del Atlántico, representan hábitat importante para muchas especies de aves migratorias (Berlanga et al. 2010). Sin embargo, México es uno de los países latinoamericanos con mayor tasa de deforestación (Askins et al. 1990). Específicamente, el estado de Veracruz tiene una alta tasa de conversión de bosques y selvas en tierra para ganadería (Barrera-Bassols 1995).

El Chipe corona negra (*Cardellina pusilla*, Parulidae) es un ave migratoria de importancia tri-nacional siendo compartida por México, Estados Unidos y Canadá (Berlanga et al. 2010) y presenta actualmente una disminución en sus poblaciones en diversas regiones de Norteamérica. Las tendencias poblacionales muestran un decremento del 1% anual para la subespecie *C. pusilla pusilla* en el este de Norteamérica y de 1.7% anual para las subespecies *C. p. pileolata* y *chryseola* en el oeste (Sauer et al. 2014). Uno de los factores asociados a su disminución es el pastoreo de ganado intensivo (Saab et al. 1995).

El estudio de marcadores genéticos en *C. pusilla* demuestra que no hay flujo genético entre los grupos de *C. pusilla* del oeste y del este y que no existen individuos con señales genéticas intermedias, además de que hay amplias diferencias genéticas (ADN mitocondrial, microsatélites, etc.) entre grupos (Kimura et al. 2002, Irwing et al. 2011) por lo cual sugieren que pueden ser especies crípticas (Irwing et al. 2011); es decir, especies altamente emparentadas o especies hermanas, comúnmente diferenciadas mediante estudios de DNA, historias de vida entre otros métodos (Elmer et al. 2007, Gómez et al. 2007). Debido a que existen diferencias genéticas entre los grupos de *C. pusilla* del oeste y del este, es posible que también presentarán distintos nichos ecológicos, que se define como el conjunto de condiciones ecológicas que pueden mantener las poblaciones sin inmigración (MacArthur 1972). El modelado de nicho ecológico aporta información ecológica que puede ayudar a la diferenciación de especies crípticas (Rissler y Apodaca 2007, Raxworthy et al. 2007, Wiens y Graham 2005).

Existen numerosos estudios de la ecología de *C. pusilla* en sus sitios de reproducción de verano (Stewart 1973, Stewart et al. 1977, Raley y Anderson 1990, Chase et al. 1997, Benson et al.

2006). En comparación la ecología invernal de *C. pusilla* en los trópicos no ha sido estudiada, el conocimiento de su actividad de invierno proviene principalmente de reportes de distribución y estudios generales de parúlidos (Hutto 1981, Lynch 1989, Rappole y Warner 1980). Durante el verano *C. pusilla* se encuentra principalmente en hábitats riparios y humedales con arbustos (Ammon y Gilbert 1999) y son más abundantes en bosques conservados que en sitios talados (Hejl et al. 1995). Existe poca información del hábitat utilizado durante el invierno, aunque se ha reportado que habita en una gran variedad de hábitats (Hutto 1981). Por ejemplo, *C. pusilla* es más abundante en bosques húmedos perennifolios de la Península de Yucatán (Lynch 1989), encontrándose también en el bosque mesófilo de montaña entre otros hábitats en Tamaulipas y Veracruz (Gram y Faaborg 1997, Ruelas-Inzunza y Aguilar-Rodríguez 2010).

Estudios realizados con otros parúlidos reportan mejor condición física de los individuos que habitan en bosques húmedos, al compararse con la condición de individuos que invernan en hábitats más abiertos como el matorral (Marra et al. 1998, Marra and Holmes 2001). Uno de los factores que influencia tal diferencia es la mayor abundancia de artrópodos en hábitats húmedos como los bosques (Latta y Faaborg 2002, Studds y Marra 2005, Brown y Sherry 2006, Studds y Marra 2007, Smith et al. 2010). Sin embargo, los efectos en las oportunidades y condición física de las aves durante la época de invierno, han sido estudiados principalmente mediante el contraste de aves que, durante esta época, se establecen en distintos tipos de hábitat (Sherry y Holmes 1996, Marra et al. 1998, Latta y Faaborg 2002, Saino et al. 2004). Se conoce muy poco acerca del efecto que tienen las variaciones en la estructura de la vegetación dadas por la perturbación humana, dentro de un mismo hábitat, sobre la ecología invernal y la condición de las aves migratorias; probablemente porque las variaciones al interior de un mismo tipo de hábitat pueden ser más sutiles y sus efectos más difíciles de probar. Revelar si existen diferencias dados los distintos grados de perturbación del hábitat, revelaría a su vez la posibilidad de que individuos invernando en distintos grados de perturbación, se desempeñaran distinto en las temporadas subsecuentes, probablemente llevando sus efectos hasta las reproducción en el siguiente verano.

Es posible que hembras y machos de *C. pusilla* defiendan territorios en sus sitios de migración de invierno, ya que en Veracruz se han reportado interacciones agresivas entre individuos y la permanencia de individuos marcados en un mismo sitio durante el invierno (Rappole y Warner 1980, Hutto 1981). Defender un territorio durante la época no reproductiva permite el acceso exclusivo a recursos alimenticios (Parrish y Sherry 1994, Sogge et al. 2007), lo cual puede significar ventajas para la supervivencia de las aves (Brown y Long 2007). La territorialidad puede variar en el rango de distribución invernal, si la disponibilidad de recursos alimenticios es cambiante (Brown y Long 2007). Asimismo, la estructura de la vegetación influye sobre la disponibilidad del alimento, siendo distinto entre sitios y creando diferencias en la accesibilidad al recurso (Maurer y Whitmore 1981, Fretz 2002). Por lo tanto, las características del hábitat de invierno, como los recursos alimenticios y la estructura de la vegetación, pueden influir en la calidad de los territorios y la condición física de machos y hembras, afectando su tiempo de llegada a Norteamérica para la reproducción (Parrish y Sherry 1994, Marra et al. 1998).

La calidad de los hábitats de invierno ha sido propuesta como un factor importante que afecta la estabilidad de las poblaciones de las aves migratorias. Sin embargo, son pocos los estudios que muestran de manera clara cómo los hábitats de invierno en los trópicos limitan a las poblaciones de aves migratorias (Marra et al. 1998). El presente trabajo provee evidencias directas para probar la hipótesis de que las características del hábitat invernal, en términos de estructura de la vegetación y abundancia de recursos alimenticios, afectan la densidad, la defensa de territorios y la condición física invernal de la especie migratoria *C. pusilla*. Así como provee evidencias de la relación entre la condición física de verano y la estructura de la vegetación, la abundancia de alimento y el tamaño del territorio invernal. Se provee información detallada de la ecología invernal de una especie cuya actividad en los trópicos, donde pasan 2/3 del año, no ha sido estudiada; a pesar de que existen numerosos estudios en sus sitios de reproducción (Stewart 1973, Stewart et al. 1977, Raley y Anderson 1990, Chase et al. 1997, Benson et al. 2006). Asimismo, se describe el nicho ecológico de verano e invierno de la especie y se establece si existen diferencias en los nichos de los grupos del Este y el Oeste de *C. pusilla*. Se espera que la información generada mediante la realización de este trabajo, sirva como herramienta en la planeación de estrategias de conservación a nivel trinacional, tanto para *C. pusilla* como para aves migratorias con necesidades ecológicas afines.

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Ecological niche variation in the Wilson's warbler *Cardellina pusilla* complex

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Wilson's warbler comprises three subspecies separated into two geographic groups: *C. p. pusilla* that breeds in eastern North America; and *C. p. pileolata* and *C. p. chryseola* that breed in western North America. Given the differences between the groups in genetics, morphology, habitat use, and population decline, we tested for ecological niche similarity in both their breeding and wintering distribution using niche modeling based on temperature and precipitation data. We first conducted an inter-prediction approach considering the percent of summer and winter localities of one group that are predicted by the potential distribution of the alternate group. We also applied a null model approach that compares self-predictions and pseudoreplicates of each group to indicate similarity, divergence, or indeterminate niche overlap. Finally, we compared ecological distances between and within groups using the Gower similarity equation. We found that the western group had an ecological niche of broader climatic conditions, while the eastern group had a narrower ecological niche. The inter-prediction approach showed that, for both summering and wintering ranges, ecological niche models of the western group predicted 50% of the observed distribution of the eastern group, whereas eastern group models predicted <18% of the western group distribution. The null model approach found that similarity in ecological niches was indeterminate, possibly due to the large area occupied by the two groups; but it suggests a more restricted set of climatic conditions of the eastern group distribution. However, the Gower coefficients demonstrated that the ecological distance between the two geographic groups was larger than the ecological distance within groups, indicating distinct ecological niches. Overall, our results support the hypothesis that the eastern and western groups of Wilson's warbler are two cryptic species; this should be taken into consideration for future analyses, particularly with respect to vulnerability categorization and conservation efforts.

There is an ongoing debate as to whether avian subspecies represent evolutionary distinct groups, and how useful the subspecies concept is for avian conservation (Zink 2004, Rojas-Soto et al. 2010). In some cases, subspecies coincide with genetic groups within species, and are a useful starting point to study divergence among populations (Phillimore and Owens 2006), particularly where pattern and coloration differences occur for isolated groups (Remsen 2010). However, trinomial nomenclature may not always accurately represent the available genetic and character variation (Fitzpatrick 2010), and in most cases subspecies classification lacks genetic or ecological basis, where erroneous classification could obscure real patterns and processes, and thus bias conservation efforts (Zink 2004). Therefore, studies are required that focus on gathering information to improve taxonomic categorization of subspecies (Ball and Avise 1992, Burbrink et al. 2000, Zink 2004, Fitzpatrick 2010, Remsen 2010, Rojas-Soto et al. 2010).

Wilson's warbler *Cardellina pusilla* (Parulidae) is traditionally thought to comprise three subspecies (AOU 1957, Lowery and Monroe 1968), which were designated based on plumage coloration and morphological size variation (Wilson 1811, Ridgway 1902, Lowery and Monroe 1968). These are separated into two geographic groups based on their summer breeding range. One subspecies, *C. p. pusilla* breeds in eastern North America (hereafter eastern group) and winters mainly in southern Texas, east Mexico, and Costa Rica. The other two subspecies *C. p. pileolata* and *C. p. chryseola* (hereafter western group) have parapatric breeding distributions in western North America (Curson et al. 1994, Dunn and Garrett 1997), and winter mainly in southwest and central Mexico through to Central America (Chapman 1907, Bent 1953, Dunn and Garrett 1997). These Wilson's warbler groups also start migration at different times and follow distinct migratory pathways (Paxton et al. 2007, 2013). Furthermore, the two western subspecies have on average larger body dimensions (Oberholser 1974, Pyle 1997), use a greater variety of breeding habitats (Eckhardt 1979, Morrison 1981, Finch 1989, Douglas et al. 1992, Ammon 1995, Dunn and Garrett 1997), and have smaller clutches (Martin 1988) than the eastern subspecies.

Nuclear and mitochondrial genetic analysis of the Wilson's warbler complex found that the eastern subspecies, *C. p. pusilla,* was strongly differentiated from both of its western counterparts, *C. p. pileolata* and *C. p. chryseola* (Kimura et al. 2002, Irwin et al. 2011, Paxton et al. 2013, Ruegg et al. 2014), while there was only subtle geographic differentiation between the two subspecies within the western population (Kimura et al. 2002, Paxton et al. 2013, Ruegg et al. 2014). These genetic differences suggest that eastern and western populations might represent two phylogenetic groups that may be cryptic species, defined as distinct species that are erroneously classified and hidden under one species name (Bickford et al. 2006). In support of this, Irwin et al. (2011) report the absence of gene flow between the groups, the lack of individuals with intermediate genetic signals, and an estimated coalescence time between groups of 2.3 million yr, which is a common divergence time for well-diagnosed and distinct species (Lovette 2005, Price 2008, Weir and Schluter 2008). Considering this scenario, research into ecological differences between the two groups could help make the case for species-level differences, which would have important conservation implications.

From a conservation perspective, the eastern and western groups of Wilson's warbler show a differentiated annual population decline (Sauer et al. 2014). We analyzed breeding bird population data for 1968–2012 from Sauer et al. (2014), which demonstrates that the western population has a significantly steeper 2.21 slope of decline compared to 1.05 decline slope for the eastern population ($F_{2,87}$ 342.6, p 0.001; Supplementary material Appendix 1, Fig. A1). This differential rate of population decline of the two groups adds to the necessity of studying each group individually to determine the causes of decline, with the possible application of distinct conservation strategies should the two groups be considered taxonomically different. Furthermore, the currently recognized single species of Wilson's warbler is considered of conservation importance in Canada, USA, and Mexico, being listed by Partners in Flight as a shared species undergoing steep population decline (Berlanga et al. 2010).

Given the morphological and genetic differences between the two Wilson's warbler subspecies groups, it is possible that these eastern and western groups may be distinct species (Irwin et al. 2011). Genetic divergence may also be associated with ecological niche divergence (Wiens and Graham 2005, Rissler and Apodaca 2007, Raxworthy et al. 2007, Zink et al. 2013). Based on the eastern and western range differences and their associated climates, we predict that these two Wilson's warbler groups will have distinct ecological niches, defined here as the environmental space that can maintain a population without immigration (Hutchinson 1957, Higgins et al. 2012), supporting the hypothesis that these represent two cryptic species. Thus, ecological niche modeling (ENM) may be a useful approach to analyze whether environmental conditions occupied by each group support the genetic differentiation of these cryptic species (Rice et al. 2003). Evidence of niche divergence, where there is adaptation to different ecological conditions (Khimoun et al. 2013), would support species-level differentiation, while niche conservatism (tendency for many ecological traits to remain similar over time; Wiens et al. 2010) would imply similitude in environmental distribution of the two groups. Alternatively, evidence of partial niche overlap suggests a degree of climatic differentiation that together with other evidence, such as the strong genetic division, could justify the distinction of eastern and western groups as cryptic species. Hence, our results could provide new evidence that contributes to taxonomic definition of this species complex, and refine conservation policies throughout the geographic range.

Methods

Database

We obtained occurrence records for the entire geographical range from the Global Biodiversity Information Facility (GBIF). Given that this database may have misidentification and geo-locality errors (Yesson et al. 2007), we thoroughly reviewed and selected the records to be used for modeling by verifying localities and dates, and eliminated 4000 records that we considered unreliable based on the source, lack of specific coordinates, or lack of coincidence with information in the literature. Records were divided into two groups: *C. p. pusilla* in the eastern group, and *C. p. pileolata* plus *C. p. chryseola* in the western group. We considered these two groups as potential cryptic species as all genetic analyses coincide in differentiating the eastern group from western populations, while there is only subtle, finer scale, geographic differentiation within the western group (Kimura et al. 2002, Irwin et al. 2011, Ruegg et al. 2014). For the summer models we considered only records during the months of June and July, while for winter models we included only records for the months of December, January and February, so as to avoid potentially including occurrence records of individuals in transit or on migration. In areas where eastern and western group distributions converge, we could only include records that specified the subspecies based on genetic evidence. These restrictions mean that for the summer distribution there was an area in central Canada where we had no locality records for the models given that the few records we gathered from this region were eventually eliminated as they either fell outside the breeding months of June and July set for the models, did not specify the subspecies, lacked coordinates, or were from unknown sources. For the winter models we excluded four records where both eastern and western subspecies of Wilson's warbler are reported to occur due to lack of precision in the record locations. While these restrictions on the records mean there may be some loss of information, we were able to use areas from which records were excluded to confirm whether the data from records included in the models was sufficient to predict as suitable for each group the areas of overlapping distribution.

To characterize the environmental niche, we obtained climatic data from the WorldClim project (Hijmans et al.

2005), upscaled at 0.01 (1 km^2). We selected the monthly maximum and minimum temperature and precipitation digital layers available for the months of June and July (summer distribution), and December, January and February (winter distribution), to obtain a maximum and minimum temperature and precipitation for both summer and winter periods. We did not include other climate data variables in the models as these were calculated for months not included in our selection of occurrence records. We are aware that using a greater number of variables could improve the description of climatic conditions for each group's niche and reduce the overprediction. Nevertheless, these three climate variables of precipitation, and minimum and maximum temperature, are known to influence avian distribution (Newton 1998, Araújo et al. 2009), and monthly data for these variables are available for the areas used by each of the three sub-species.

Ecological niche modeling

To model the summer and winter ecological niches of the two groups of Wilson's warbler we applied MaxEnt (ver. 3.3.3k, Phillips et al. 2006), using the previously validated occurrence records. For the summer models we used 632 western occurrence records and 189 eastern occurrence records, while for the winter models we used 15 western occurrence records and 102 eastern occurrence records. Given that the two Wilson's warbler groups occur together in several wintering grounds, we used only the genetically confirmed winter occurrence records (Kimura et al. 2002, Irwin et al. 2011). In the case of the eastern group, given that the sample size would have been too small using only genetically confirmed occurrences, we also used locality records obtained from the literature (Curson et al. 1994, Dunn and Garrett 1997). Prior to running models we withheld 30% of occurrence records, which were later used as distinct records for validating the final models.

MaxEnt uses the maximum entropy principle to calculate a probability distribution for each pixel, which can be interpreted as a habitat suitability index for the population being modeled (Elith et al. 2011). We used the MaxEnt default of 500 iterations which was sufficient for the models to reach convergence, and is the default level used by background test models in ENMTools. We also fixed a 0.00001 convergence limit, and a regularization value of 1. We set 10 replicates, and set a 'random test percentage' of 20% of records to be selected by MaxEnt as a separate subset for internal validation. To select the best self-prediction (niche model prediction on the area corresponding to the occurrence localities used to set the environmental conditions), we chose the model with the lowest rate of omission, and the highest value of area under the curve (AUC) of the receiver operating characteristic (ROC; Phillips et al. 2006). MaxEnt results are given in probability values that range from 0 to 1, indicating the relative suitability of the geographic representation of ecological space. These values were transformed to a binary absence–presence map, using a 10% threshold of acceptable omission error that shows the total suitability area predicted for the population. We chose the lowest rate of 10% omission error since selecting a higher percentile of omission error reduced even further the predicted area of the binary model, leaving-out several confirmed and well-known occurrence localities (e.g. Burrough Valley and Placer County, CA, under 20% TP). Moreover our previous occurrence record validation had already eliminated some of the possible model inaccuracies.

The performance of MaxEnt models is traditionally evaluated using the AUC values (Phillips et al. 2006) which allows evaluation of the coincidence of climatic suitability generated by the model with the known occurrences, where 1 indicates perfect discrimination and 0.5 indicates that the discrimination is no better than the suitability given by a random assumption (Fielding and Bell 1997). However several problems have been associated with this technique (Lobo et al. 2008, Peterson et al. 2008), one being that the two error components (omission and commission) are inappropriately weighted equally. Therefore, we used the partial-area ROC approach that solves this problem by evaluating only over the spectrum of the prediction, and allowing a differential weighting of the two error components (Peterson et al. 2008, Williams and Peterson 2009). For each model we calculated partial AUCs using the Tool for Partial-ROC ver. 1.0. (Barve 2008). AUCs were limited to the proportional area over which models actually made predictions, and only omission errors 5% were considered (Peterson et al. 2008). The results of the partial ROC curves demonstrated that the performance of the three models was significantly greater than expected at random: eastern summer self-prediction (AUC ratio 1.40, p 0.001); eastern winter self-prediction (AUC ratio 1.64, p 0.001); and western summer self-prediction (AUC ratio 1.27, p 0.001).

Only in the case of the western winter self-prediction model we could not apply partial-ROC AUC calculation due to the low number of occurrence records available. Therefore, to aid validation of the western winter self-prediction, it was desirable to distinguish 'suitable' from 'unsuitable' areas by setting a decision threshold above which model output is considered to be a prediction of the species presence. The selection of the threshold depends on the data used or the objective of the map, and varies from species to species (Pearson et al. 2004). We followed the settings suggested by Pearson et al. (2007) for small samples of occurrence records, where we made 15 predictions, with one of the observed localities excluded in each case. For each prediction, two threshold decisions were applied (minimum training presence and fixed cumulative value of 20), and the ability to predict the excluded locality was tested. We calculated a p value for the overall model across the set of jackknife predictions using the script provided by Pearson et al. (2007). The projected potential Wilson's warbler western winter distribution model was trained using 15 localities that had high and significant success rates in jackknife tests with a threshold of 10% (T10 0.24, p 0.04), and minimum training presence of MTP 0.31, p 0.04. Given that both tests had the same significance value, we selected the fixed cumulative value (T10) because the minimum training presence produced a larger predicted area that included areas where Wilson's warbler is known not to occur.

Niche similarity

We used three approaches to determine whether eastern and western groups of Wilson's warbler have distinct ecological niches. The first two approaches have been used previously to evaluate niche similarities, while the third approach is an application of the Gower coefficient equation used to compare ecological distance within and between groups as a measure of niche similitude (Hijmans et al. 2004).

Inter-prediction approach

To obtain the inter-prediction percentage between eastern and western niches we followed the method used by Peterson et al. (1999). For both summer and winter, we counted all the eastern occurrence localities that fell within the predicted potential western distribution model (under the 10% training presence threshold), and calculated the inter-prediction percent of eastern records that were predicted by the western ecological niche. This was then repeated for the western occurrence records.

Null model approach

We used a background similarity test performed in ENMtools to evaluate the differences in similarity between observed niches relative to the differences between observed, and random or background niches (Warren et al. 2008, 2010). For the summer and winter comparison, we used climatic data from the same occurrence records used for the MaxEnt models, and the inter-prediction percentages. We defined raster distribution areas as background areas for both groups by modifying the distribution maps from Irwin et al. (2011) through conservatively using the free-hand method to include occurrence records that were previously validated for summer and winter distributions. This was to ensure that we did not include unconfirmed distribution areas, thereby avoiding overestimation of environmental conditions.

The background test generates a MaxEnt self-prediction ENM f for each of the eastern and western groups, projecting the climatic features of the occurrence records onto the distribution area of the corresponding group (Phillips et al. 2006). The background test also generates MaxEnt ENM random projections that represent pseudoreplicates of the geographic distribution of each group. To generate pseudoreplicates from the eastern background area, the program randomly selects localities to match the number of western occurrences; the opposite is done to generate western pseudoreplicates. We performed 100 pseudoreplicates for each group because this typically suffices to evaluate and contrast with high confidence the null and alternative hypothesis (Warren et al. 2008). These pseudoreplicates were compared with the self-prediction conditions for the alternate eastern or western group. We used ENMTools to generate the Hellinger-based I similarity statistic (Van der Vaart 1998) for each pseudoreplicate, thereby creating two null distributions of niche similarity values, one comparing eastern observations with western random, or background niche, and the second in the opposite direction comparing western observations with eastern background niche (Warren et al. 2008). We used the I similarity values for comparisons that range from 0 to 1, as this index is statistically robust (Thompson et al. 2011). Finally using the overlap test a similarity measure is obtained by intersecting the original self-predictions of the two groups, which is considered the 'observed' value.

The observed I similarity value was compared to the pseudoreplicate similarity values and represented on a histogram. When the observed value falls outside the range of values obtained from the pseudoreplicates of each group, this can indicate either niche similarity or divergence. Failure to reject the null hypothesis, when variation between niche overlap and background is indistinguishable, may indicate insufficient power to determine niche differentiation or conservatism due to sample size or habitat distribution (Warren et al. 2008). An observed value closer to 1 indicates similarity, while a value closer to 0 indicates divergence (Phillips et al. 2006). However if the observed value falls within the range of the pseudoreplicate values on the histograms, then it is not possible to distinguish the observed similarity value from those generated by random niche comparisons. Nevertheless, the background test can show a partial differentiation even when the test does not clearly demonstrate similarity or divergence in ecological niche. This can be determined when the observed value falls outside the interval of values obtained from random predictions of at least one of the groups (McCormack et al. 2010, Zink 2014).

Ecological distance approach

In addition to the inter-prediction and background approaches, we evaluated eastern and western niche similarity during summer and winter, by measuring ecological distance of occurrence records within and between groups using the Gower similarity equation (Gower 1971):

$$d_{rs} = \sum_{i=1}^{3} \frac{|y_{ri} - y_{sj}|}{R_j}$$

In this study, y represents the climate vector of precipitation, minimum temperature, and maximum temperature. Where y_r (y_{r1}, y_{r2}, y_{r3}) is the climate vector of the rth occurrence, and y_s (y_{s1}, y_{s2}, y_{s3}) represents the climate vector in another occurrence location. Rj is the range of the three climate variables, where R_1 is the range of precipitation (the difference between the maximum and minimum precipitation), R_2 is the range of minimum temperatures, and R_3 is the range of maximum temperatures.

We used Gower metrics since this has been successfully used for ENM by the DOMAIN procedure, and quantified similarity between two sites using range standardization to equalize the contribution of each climatic variable (Carpenter et al. 1993). We obtained and compared Gower coefficients for the eastern and western summer and winter climatic conditions. First we calculated the ecological distances between each occurrence record of group A (eastern group) to every other record of the same group, and the same was done for group B (western group). We then calculated the average ecological distance between occurrence records within both groups to get the ecological distance within group A and the ecological distance within group B. Secondly, we obtained the ecological distance of each occurrence record of group A to every occurrence record of group B, and calculated the average ecological distance between occurrence records of the two groups to get the ecological distance between group A and B. This provided three values: 1) the average ecological distance within group A, 2) the average ecological distance within group B, and 3) the average ecological distance between groups A and B. We expected that if the ecological niche conditions of the two groups were distinct, then the distance between groups would be larger than the distance within each group.

Results

Inter-prediction

The distributions generated by ENM demonstrated some overlap in ecological and geographic space for summer breeding ranges (Fig. 1). The ecological niche self-prediction for the western group of *C. p. pileolata/chryseola* predicted 56.1% of eastern summer occurrence records and included a large portion of the eastern group *C. p. pusilla* distribution (Fig. 1A). On the other hand, the eastern ecological niche self-prediction coincided with only 17.5% of the western occurrence records (Fig. 1B). We also found some niche overlap for the potential winter distribution (Fig. 2), where the ecological niche self-prediction for the western group predicted 51.4% of eastern occurrences (Fig. 2A), but the eastern ecological niche self-prediction coincided with only 6.7% of western occurrences (Fig. 2B). Additionally we corroborated that the excluded localities, where both eastern and western Wilson's warbler co-occur, were predicted for both groups' winter self-predictions, validating our results.

Null model of similarity

The null models approach allowed us to partially differentiate eastern niche from western niche. The values from the comparison of eastern and western niche models were closer

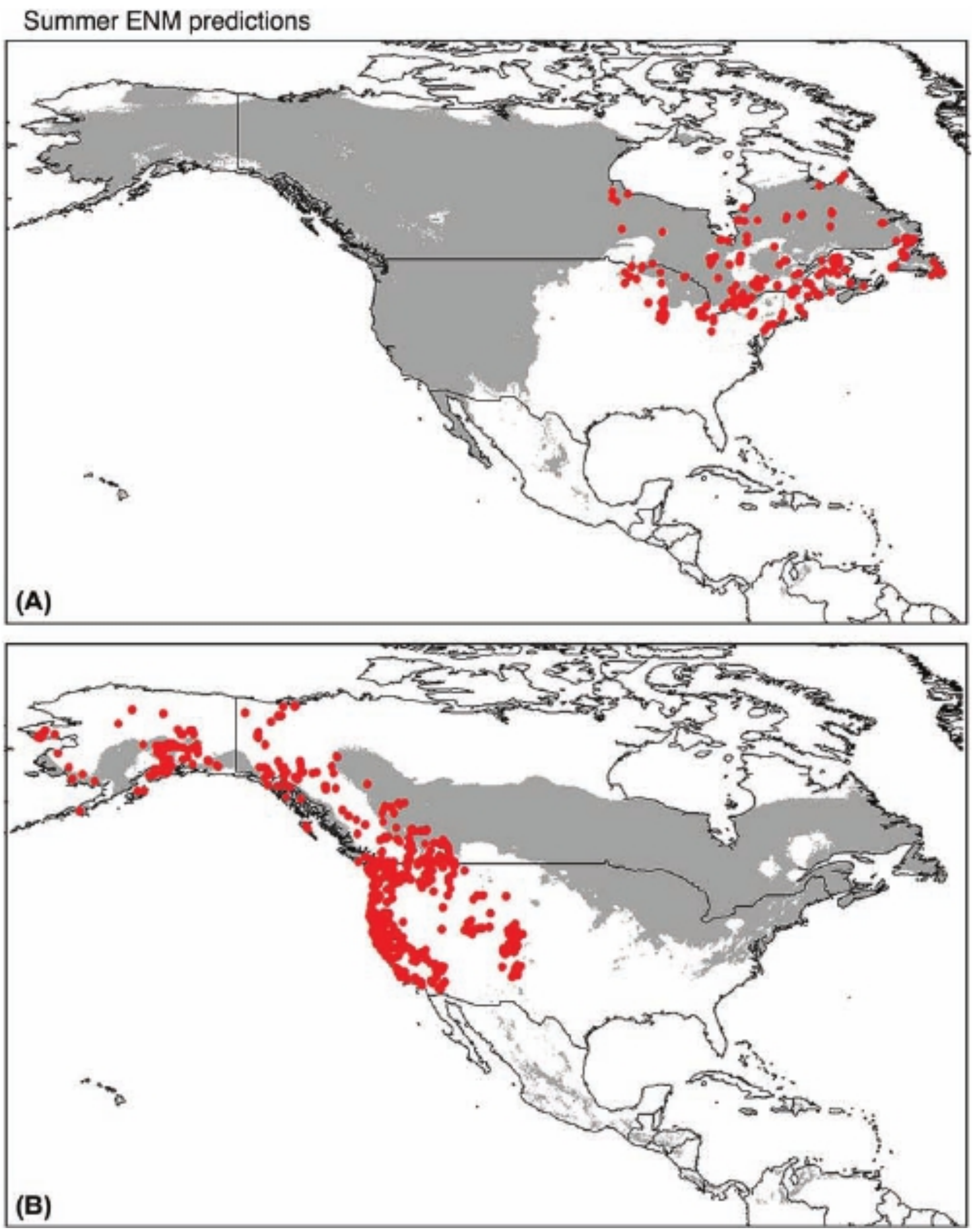

Figure 1. MaxEnt self-predictions of Wilson's warbler summer breeding distribution for (A) western self-prediction showing eastern occurrences, and (B) eastern self-prediction showing western occurrences. Prediction area is shown in gray shading, and occurrence records are shown as red dots.

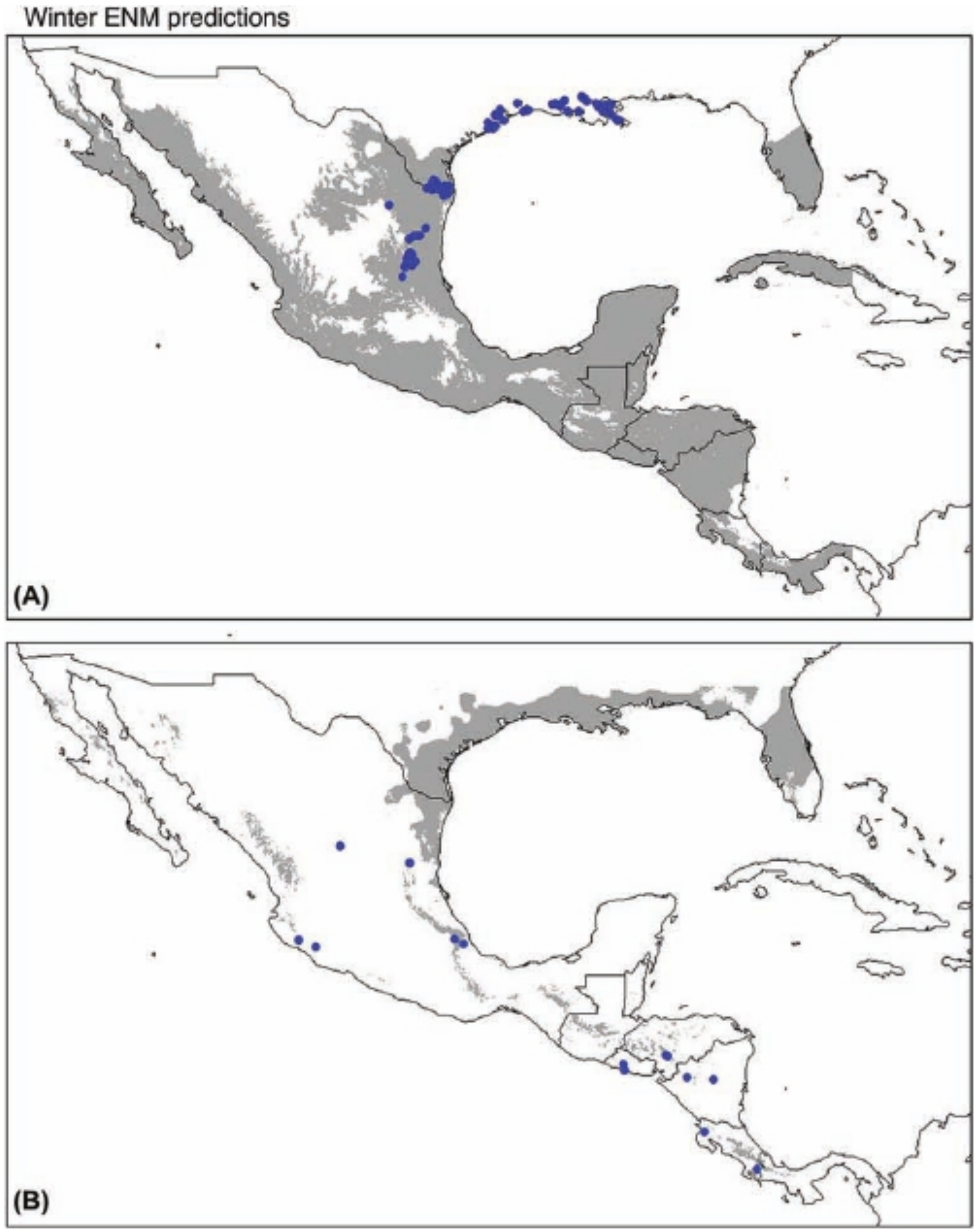

Figure 2. MaxEnt predictions of Wilson's warbler winter distribution for (A) western self-prediction showing eastern occurrences, and (B) eastern self-prediction showing western occurrences. Prediction area is shown in gray shading and occurrence records are shown as blue dots.

to 0 than the values obtained by comparing eastern background conditions to western actual niche model (Fig 3). However, no differences were evident for the reverse comparison of western background conditions against eastern actual niche model (Fig. 3). This differentiation of eastern niche is determined because the overlap values from the comparison of summer (0.61; Fig. 3A) and winter (0.51; Fig. 3B) self-predictions fell outside the range of null distribution values obtained from the eastern random projections compared to the western self-prediction (summer: 0.79–0.83; winter: 0.78–0.88; Fig. 3), but occurred within the range of null distribution values for the western random projections compared to eastern self-prediction (summer: 0.53–0.64; winter: 0.43–0.59; Fig. 3). Hence, summer and winter self-prediction overlap values differentiated from the null distribution similarity values of the eastern random projections, but were indistinguishable from the null distribution values of the western random projections.

Partial niche differentiation is explained by variation in the environmental conditions available to one group within the range of the second group suggesting that climatic conditions for the western occurrence records are distinguishable from the eastern background conditions, but that conditions for the eastern occurrence records are usually predicted by the variation in climatic conditions of the western background. Furthermore it is possible to infer that the eastern background has lower climatic heterogeneity than the western background, since the eastern null distribution has a smaller range of values than the western null distribution, particularly in the summer. A more restricted

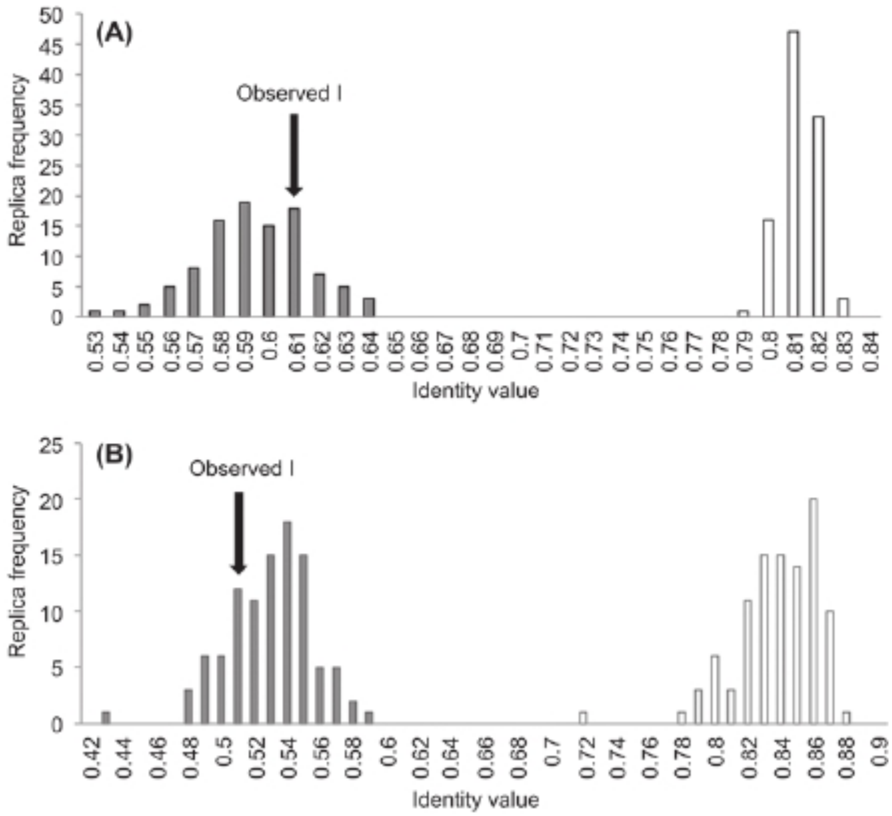

Figure 3. Distribution of 100 random values of Warren's *I* for (A) the summer samples from eastern and western groups, and (B) the winter samples from eastern and western groups. In both cases arrows show the Warren's *I* value for the self-predictions overlap (observed value), indicating neither niche divergence nor niche conservatism. White bars represent pseudoreplicates using random occurrences from the eastern distribution background and gray bars represent pseudoreplicates using random occurrences from the western distribution background.

set of random similarity values would be expected for a background with more homogenous environmental conditions, while a background with heterogeneous environmental conditions would have a broader range of null distribution similarity values.

Ecological distance test

The ecological distance in climatic niche conditions between eastern and western groups was larger than the distance within each group for both summer and winter occurrence records. In summer, the ecological distance between groups was 0.82, which was larger than the distance within eastern (0.68) and western (0.66) groups. In the case of the winter distribution, the ecological distance between eastern and western occurrence records was 1.24, which was also larger than the within-group distances for the winter distribution (eastern 0.88; western 0.84). These differences in eastern and western niches can be appreciated when represented in a three-dimensional graph of ecological space, defined by maximum temperature, minimum temperature and precipitation. During both summer and winter, the eastern group occurs in areas with higher precipitation and lower temperature compared to the western group (Fig. 4). Of the three climatic variables used, precipitation seems to have a greater effect in separating ecological distributions of the two Wilson's warbler groups (Fig. 4).

Discussion

In this study, we evaluated the ecological niche similarity of Wilson's warbler eastern and western groups to assess whether these genetically differentiated groups differ in their ecological niches. The inter-prediction percent, the null model test, and the ecological distance comparison of the two geographically distinct Wilson's warbler groups suggest that the eastern and western groups have partially differentiated ecological niches. We found differences between groups in the climatic conditions occupied during both summer and winter. Furthermore, the climatic data shows that the ecological niche of the western group is broader with regard to temperature and precipitation than that for the eastern group, which has a distribution with more restricted climatic features. Hence, based only on temperature and precipitation, both subspecies groups could co-occur within a considerable portion of the eastern group summer geographic distribution, particularly in central and eastern Canada. However, this large overlap in distribution has not been reported (Irwin et al. 2011), and the summer distributions of the two geographic groups remain parapatric.

Environmental factors other than climatic conditions may be responsible for the distinct geographic distributions of eastern and western groups of Wilson's warbler. Plasticity in habitat use may influence distribution as the western group is able to breed in a broader spectrum of habitats

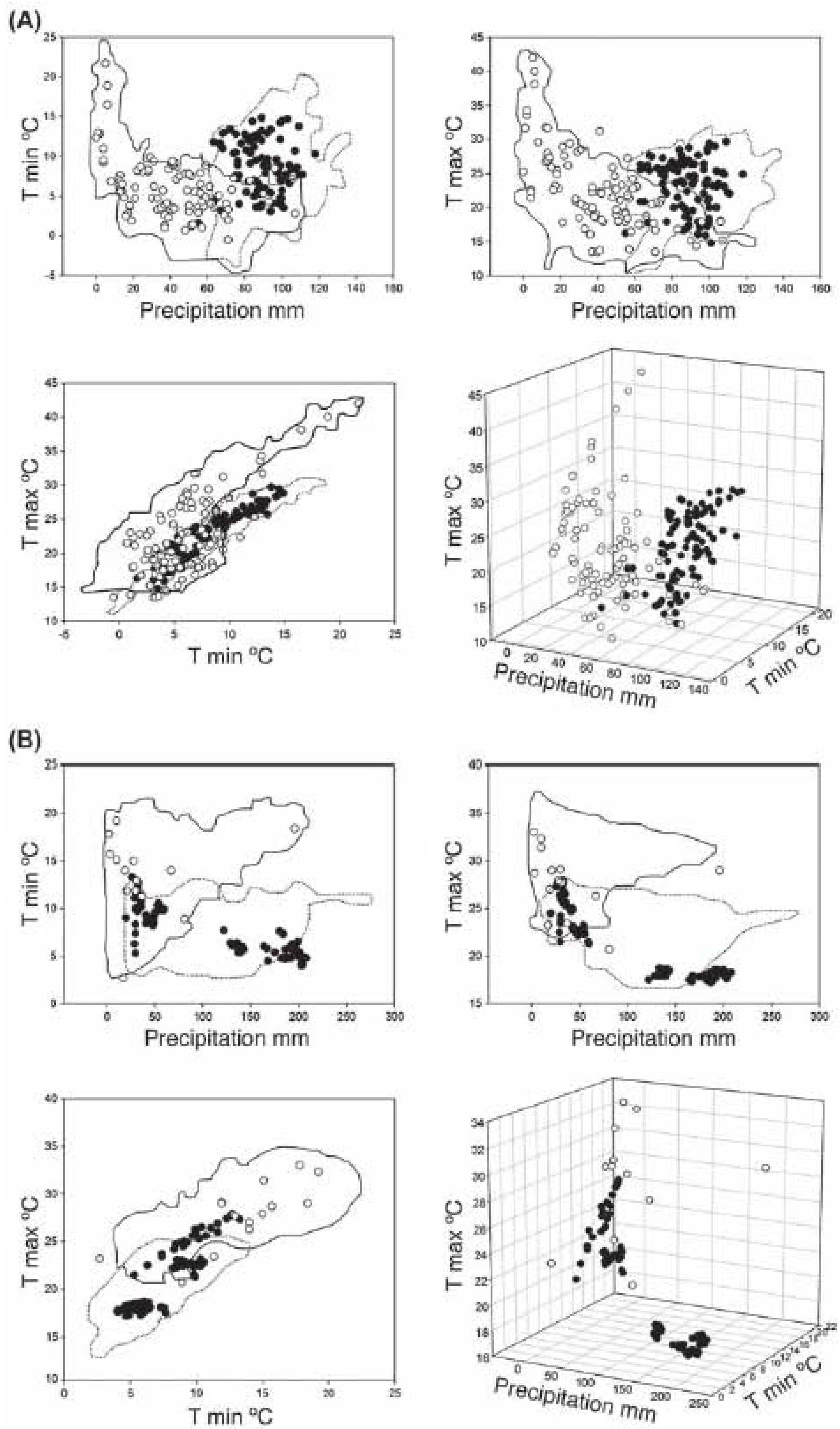

Figure 4. Summer (A) and winter (B) bi-dimensional and three-dimensional display of maximum temperature, minimum temperature and precipitation for the occurrences of eastern (black dots) and western (white dots) groups, and for 1000 random points taken from each corresponding group self-prediction. The area covered by the random points is shown as a cloud. Western cloud is shown as a black line, and eastern cloud is shown as a dotted line.

(dense and humid tree stands with limited canopy cover, high understory shrub cover, and even xeric shrubby areas; Morrison 1981, Finch 1989, Douglas et al. 1992) than the eastern group (swamps, early successional forests, and clearings; Morrison 1981, Finch 1989, Douglas et al. 1992, Dunn and Garrett 1997). The western group is also distributed over a larger area during the winter, including most of Mexico, compared to the eastern group which is restricted to southern Texas, east Mexico, and Costa Rica, as shown by our ENM potential geographical distributions and the literature (Chapman 1907, Bent 1953, Dunn and Garrett 1997). This coincides with the use of a broader range of temperature and precipitation conditions by the western group, since environmental heterogeneity increases when the species' range increases (Nakazato et al. 2010). Hence the use of remote-sensing layers that provide information on vegetation could improve the ability to discriminate the niches of the Wilson's warbler groups. However the use of vegetation layers could also add uncertainty to the models if the layers are not selected properly due to a lack of correspondence between the available layers and the occurrence data. Generally, the historic occurrence data comprise more than a century of field registries, and the vegetation frequently suffers modifications within that time, causing a lack of coincidence between the vegetation existent when individuals were registered, and the vegetation layer shown in those localities.

As well as abiotic factors, biotic interactions such as interspecific territory avoidance may also influence the distinct geographic distribution of the two Wilson's warbler groups. Birds may defend territories from individuals of other species where these are potential competitors, and given the investment of time and energy this demands, natural selection eventually favors ecological divergence. This type of avoidance occurs between the species of greatest morphological similarity, and has been studied in other warblers (Bourski and Forstmeier 2000). However, biotic interactions are generally not included in ecological niche models due to the difficulty of obtaining the necessary data, and the fact that they act at a finer scale (Pearson and Dawson 2003), making this difficult to demonstrate.

The considerable area of ecological niche overlap for eastern and western groups of Wilson's warbler could be due to the plasticity of a generalist complex such as Wilson's warbler that occupies a diverse set of environments, and as a result of a common ancestry of the two groups. Ecological niche modeling may experience difficulties in accurately predicting the niche of a generalist species, as the use of a broad set of environments may lead to model inaccuracies of over-prediction (Seoane et al. 2005, Evangelista et al. 2008). However, these models are still useful to identify suitable habitats and potential distributions (Evangelista et al. 2008). Moreover species with recent common ancestry are more likely to present niche similarities, since they could show a tendency to resemble each other more than they resemble other species not related or distant in phylogeny, a trait known as the phylogenetic signal (Blomberg and Garland 2002).

In our study, the background test could not determine similarity or divergence in the ecological conditions occupied by the two Wilson's warbler groups given the variation in ecological conditions from the random projections. This inconclusive result could be attributed to the large variability of environmental conditions within the modeled area, which includes most of Canada and the United States for the summer models, and south of the United States, Mexico and Central America for the winter models. A less inclusive background area might lead to narrower null distributions with a greater possibility of rejecting similarity. Nevertheless, as explained by McCormack et al. (2010) and Zink (2014), even when neither niche conservatism nor niche divergence can be determined by the test, it may be possible to distinguish partial differentiation.

In our study, the inter-prediction and the null model approaches indicate that the eastern ecological niche is narrower than the western ecological niche, and that western climatic conditions are more likely to predict eastern occurrences than the reverse prediction. Nakazato et al. (2010) suggest that the unidirectional differentiation of two species with no overlapping distribution, such as Wilson's warbler groups, may occur as each species occupies a subset of the habitats available within their distribution, which may be more varied for the species with a larger distribution, and more likely to include a subset of the habitat occupied by the species with the smaller distribution. Hence, the unidirectional difference in Wilson's warbler groups could be due to the specificity of climatic conditions in the smaller distribution of the eastern group when compared to the broader climatic conditions in the larger distribution of the western group.

It should be taken into account that results of the background test are particularly sensitive to background definition. The suite of habitats available for each species increases as the background increases (Nakazato et al. 2010), therefore background definition is critical to avoid over and under estimations of similarity. In the case of the Wilson's warbler, we are confident that we have reduced errors to the minimum, since we used the well-known distribution area of western and eastern groups (Irwin et al. 2011), and additional localities that were not present in this distribution were only included after carefully validating the occurrence records.

The use of the Gower similarity equation provided an efficient and informative index to test for niche differences that can be interpreted as differences in size and position in ecological space between niches. In the present study, the magnitude of the difference in average ecological distance between groups compared to average distance within groups provides confidence in interpreting ecological niches as dissimilar, even though the test may be limited in that it does not provide a definitive statistical answer. However it is important to take into consideration that although the Gower equation is a helpful tool to quantify divergence, it does not take into account the autocorrelation of climatic data as does the null model approach, and it does not test for significance.

The three different approaches used to test niche similarity between eastern and western Wilson's warbler groups strengthen the findings of this study, and coincide in suggesting partial niche differentiation of the two groups. Thus, our results support the Irwin et al. (2011) proposal that the Wilson's warbler complex should be considered as two cryptic independent species, consistent with other genetic (Kimura et al. 2002) and habitat differences (Morrison 1981, Finch 1989, Douglas et al. 1992, Dunn and Garrett 1997). A recent study by Ruegg et al. (2014) supported the eastern population as a single group genetically distinct to western populations, but found five genetically variable groups within the western group. This suggests that there may be a finer scale division within the western group that could be explored in the future to elucidate the broad environmental conditions occupied by this group. Hence, genetic and morphological studies of the Wilson's warbler complex (Pyle 1997, Irwin et al. 2011, Paxton et al. 2013, Ruegg et al. 2014) coincide in considering that the eastern group is not subdivided and differs from the western group, which is subdivided into two or five different groups depending on the approach of the study. This could explain why our results show that the eastern group seems to be ecologically and geographically more restricted than the western group. These findings indicate that the ecological niches of eastern and western Wilson's warbler groups fit the partial ecological niche divergence pattern (Peterson and Holt 2003), and add to the evidence for the cryptic species hypothesis proposed by Irwin et al. (2011). Hence, eastern and western populations seem to be two species where the eastern group has a more restricted ecological and geographic distribution.

The Wilson's warbler complex is considered a widespread and generalist species within North America (Hutto 1981, Berlanga et al. 2010). However, the fact that the groups within the complex may be cryptic species means that they probably fall into more specific habitat use categories, and they need to be recognized and more thoroughly studied. It is noteworthy that regardless of an apparently greater ecological plasticity and broader use of breeding and wintering grounds, the western group shows a significantly higher rate of population decline than the eastern group (Sauer et al. 2014). Thus evidence of morphological, genetic, and ecological differences within the Wilson's warbler complex should be taken into consideration when determining future vulnerability categorization and directing conservation efforts. This is particularly relevant as other subspecies have been awarded separate protection criteria, even when such cases may not have as many ecological, genetic, and morphological differences as found for Wilson's warbler (U.S. Fish and Wildlife Service and National Marine Fisheries Service 1996, Rojas-Soto et al. 2010, Zink et al. 2013, Zink 2004). Fitzpatrick (2010) states that in order to pursue rational conservation policies, we should adopt a more rigorous analysis of distinctiveness between biological entities that takes into account ecological, genetic, behavioral, and evolutionary distinctiveness. This in turn will enable stronger subspecies categorization (Ball and Avise 1992, Burbrink et al. 2000, Zink 2004, Fitzpatrick 2010, Remsen 2010, Rojas-Soto et al. 2010).

Wilson's warbler may have distinct migratory and breeding ecologies as during the winter Wilson's warbler occurs from southern USA to Central America in a diverse set of environments, such as tropical evergreen and deciduous forest, cloud forest, pine-oak forest, forest edge, mangroves, brushy fields and plantations, distinct to those occupied in the summer (Hutto 1981, Lynch 1989, Gram and Faaborg 1997, Ruelas-Inzunza and Aguilar-Rodríguez 2010). Considering the migratory strategy of Wilson's warbler, and that we also determined niche divergence between eastern and western groups in winter, further studies should address possible differences in migratory ecology of the two groups. Geographic migratory routes may also vary, as Wilson's warbler populations from different breeding latitudes exhibit temporal variations in transit through a migratory stopover site (Paxton et al. 2007, 2013). Hence, ecological niche divergence could not only be affecting summer and winter distribution, but also spring and autumn population movements. This approach could encompass ecological questions in an adequate space-time scale, and help unveil underlying processes affecting continental-wide population trends.

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Supplementary material (Appendix JAV-00531 at www.avianbiology.org/readers/appendix). Appendix 1.

Winter habitat disturbance influences density and territory size of a Neotropical migratory warbler

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Abstract

Migratory birds face population declines attributed to habitat loss and modification in the wintering grounds, which may influence body condition, time of arrival to breeding grounds, and future reproductive opportunities. Despite this, very little is known of wintering ecology of migratory birds. During three winter seasons, we assessed Wilson's Warbler (*Cardellina pusilla*) density, territory size, and body condition at three cloud forest sites with differing degrees of habitat disturbance and forest cover: i) preserved 125 ha cloud forest actively protected for 40 yrs; ii) moderately disturbed site of 67.5 ha cloud forest under protection for 29 years; and iii) highly disturbed unprotected site with 6.5 ha cloud forest. We determined warbler density using 20 unlimited-radius point-counts at each site. We also captured and measured a total of 74 birds over three years to obtain an indicator of body condition, and re-sighted color-banded birds to determine individual territory size at each site. We found significantly higher bird density in the conserved forest site, which was double that found in the disturbed sites with lower forest cover. Territory size also varied significantly among sites, with smaller territories in the conserved forest compared to the disturbed forest sites where territories were larger. However, there was no significant difference in body condition of territorial birds among forest disturbance sites. Furthermore, territory size and body condition was relatively constant among years for birds in conserved forest, but exhibited high inter-annual fluctuation for birds in disturbed forest sites. Considering the higher bird density, smaller territory size, and inter-annually consistent body condition at the conserved cloud forest site, we propose that this represents higher quality wintering habitat for Wilson's Warbler and other migratory birds.

Keywords: body condition, *Cardellina pusilla*, cloud forest, vegetation structure, Wilson's Warbler, winter ecology.

Introduction

Over the last two decades, there has been an evident population decline in Neotropical migratory birds (Robbins et al. 1989; Askins et al. 1990, Ballard et al. 2003, Sauer et al. 2014), while resident bird species do not show a similar trend (Rappole and McDonald 1994). These population declines seem to be correlated with habitat loss on the wintering grounds (Robbins et al. 1989; Askins et al. 1990), and is further suggested by a decrease in individuals returning to breeding areas after migration (Rappole and McDonald 1994), with a decline in occupancy of suitable nest-sites (McShea et al. 1995). It has therefore been suggested that population dynamics of Neotropical migratory birds has been negatively influenced by processes occurring in the wintering grounds (Rappole and McDonald 1994).

Wintering habitat quality may determine the physical condition, survival, and reproductive fitness of birds (Marra et al. 1998; Marra and Holmes 2001; Gunnarsson et al. 2005). Individuals of the American Redstart (*Setophaga ruticilla*) that occupy higher quality mature mangrove forest sites during the winter in Jamaica, have better physical condition and arrive first to breeding territories, thereby increasing their chances of breeding success, compared to individuals occupying suboptimal sites of second-growth scrub (Marra et al. 1998; Marra and Holmes 2001). However, there is a lack of knowledge on wintering habitat use of migratory birds in the tropics, which could vary greatly among species (Rappole and McDonald 1994; Marra et al. 1998; Brown and Long 2007). Notably, the largest population decline has been registered for birds that use forest habitats during the winter, compared to populations that inhabit vegetation of open areas (Robbins et al. 1989).

In general, it is expected that population size would be higher in higher quality habitats (Gilroy and Sutherland 2007). Accordingly, density has been positively correlated with resource abundance (Greenberg 1992; Lefebvre et al. 1994; Lefebvre and Poulin 1996) and body condition (Sherry and Holmes 1996). Furthermore, even when studies have not found a positive correlation of bird density with body condition and food abundance (Marra and Holmes 2001; Hart et al. 2011), it can be an informative parameter to explore habitat quality if accompanied by the study of other variables (van Horne 1983; Vickery et al. 1992). Migratory birds that maintain territoriality during the winter may be expected to follow the same pattern of higher densities and smaller territories in better quality habitats.

Wilson’s Warbler is a migratory species that inhabits forested habitats throughout its range, and exhibits territoriality both in breeding and wintering grounds (Eckhardt 1979; Ammon and Gilbert 1999; Rappole and

Warner 1980; Hutto 1981). Wilson's Warbler is of importance for Canada, United States, and Mexico, being listed as a tri-national shared species undergoing steep population decline (Berlanga et al. 2010). This population decline has been primarily related to intensive livestock grazing (Saab et al. 1995), demonstrating a 2.21% annual decline for the western population of Wilson's Warbler (Sauer et al. 2014; Ruiz-Sánchez et al. 2015). During the breeding season, Wilson's Warbler appears able to occupy both regenerated forests and clear-cut areas (Hejl et al. 1995; Desrochers et al. 2012). However, the ecological requirements of Wilson's Warbler are likely to differ between the breeding and wintering season. The species is found in more habitats during the winter (Hutto 1981, 1994; Stiles et al. 1995) than in the summer (Eckhardt 1979; Finch 1989), and migratory birds may change their feeding habits between summer and winter seasons (Long and Stouffer 2003; Pierce and McWilliams 2005; Martins et al. 2013). Therefore, habitat requirements are likely to vary between the summer breeding season and winter migration. At a stopover point in New Mexico, Yong et al. (1998) found that adult Wilson's Warblers were more frequently captured in forest habitats where they had positive rates of fat deposition, whereas birds in agricultural field and edge habitats had the lowest rates of fat deposition and longer stopover times. Therefore, forest habitats may be more favorable to the species during the winter migration.

Studies on winter dynamics could give an insight to the species' population decline, since there could be negative effects on Wilson's Warbler populations of habitat modification in the wintering areas. Carry-over effects from wintering habitats for breeding success of migratory birds have been repeatedly proven (Marra et al. 1998; Norris et al. 2004; Reudink et al. 2009), although these have mainly been based on comparisons of birds wintering in different types of habitat (Sherry and Holmes 1996; Marra et al. 1998; Latta and Faaborg 2002; Saino et al. 2004). Little is known of the possible effects of changes in vegetation structure due to human disturbance on the wintering ecology and condition of migratory birds within the same habitat-type. Therefore, in the present study we assessed Wilson's Warbler winter density, territory size, and body condition in three cloud forest sites with differing degrees of habitat disturbance and forest cover. We expected that Wilson's Warblers in conserved cloud forest would present higher bird densities, smaller territory size, and improved body condition compared to birds wintering in disturbed cloud forest fragments.

Methods

Study area

The study was conducted in the cloud forest of central Veracruz, considered an Important Bird Area (Arizmendi and Marquez Valdelamar 2000). We sampled three sites with varying degrees of forest modification that were separated by 5-11 km. The conserved forest site was located in the Santuario de Bosque de Niebla Francisco Javier Clavijero (19.5º N, 97.02º W). This is a protected cloud forest sanctuary managed by the Instituto de Ecología since 1976, and comprises 125 ha of continuous forest surrounded by secondary-growth cloud forest. The moderately disturbed site was located in "El Tejar Garnica", Xalapa (19.52º N, 96.89º W), an area under protection since 1986, which is composed of 67.5 ha of mature cloud forest surrounded by secondary-growth, grassland, and urban areas. Finally, the highly disturbed site occurred in Rancho El Trébol, Banderilla county (19.59º N, 96.97º W), and comprised a 6.5 ha cloud forest fragment immersed in a matrix of farmland and secondary-growth. The region has a temperate-humid climate with mean temperature of 18°C, and year-round rainfall of 1500-2000 mm annually (Williams-Linera et al. 2013). All sites were located within an altitudinal range of 1320-1690 m above sea level to reduce potential effects due to altitudinal variation.

Forest structure

To evaluate the influence of habitat modification on forest structure at the three sites, we measured five variables of the woody vegetation that are among the first features to be altered or removed: tree height, shrub height, tree basal area, tree abundance and shrub abundance. We establish one 25 m-diameter circular plot in each territory of a marked Wilson's Warbler (Blake and Hoppes 1986), obtaining a total of 30 plots in the conserved forest site, 26 plots in the moderately disturbed site, and 24 plots in the highly disturbed site. Within each plot, we counted all individuals to determine tree and shrub abundance, and calculated tree and shrub height using a clinometer (Suunto PM-5). We also estimated tree basal area for each Wilson's Warbler territory by variable radius plot sampling using an angle gauge (JIM-GEM® Cruz-All) with an English basal area factor of five. In this way, we multiplied by 5 the total number of hits of trees with diameters greater than the edges of the angle-gauge, determined from the center of the sample plot.

Bird density

To determine density of Wilson's Warblers, we established 20 variable radius point-counts at each site (Buckland et al. 1993), with a separation distance of 200 m between point-counts. One observer (ARS) conducted all point-counts during the month of January in the winters of 2011-2012, 2012-2013, and 2013-2014. However, only 8 point-counts were conducted at the highly disturbed site of Trébol during the first winter of 2011-2012. A count duration of 5 min was used at each point-count, during which we recorded all Wilson's Warbler individuals that were detected both visually and acoustically (Ralph et al. 1996). The distance from the observer to each bird located was measured with a range finder (Vortex Ranger 1000).

Body condition

We used mist-nets and the play-back method (Johnson et al. 1981) to capture territorial Wilson's Warbler individuals at each site. Up to four mist-nets of 12 m length and 32 mm mesh were set-up within the territory of each Wilson's Warbler individual. Over three seasons we captured a total of 72 individuals with 2 recaptures, giving a total of 74 body condition measurements: 29 in the conserved forest site (2011-2012 = 10, 2012-2013 = 10; 2013-2014 = 9); 25 captures in the moderate disturbance site (2011-2012 = 6, 2012-2013 = 9; 2013-2014 = 10); and 20 captures in the highly disturbed site (2011-2012 = 2, 2012-2013 = 8; 2013-2014 = 10). Captures where conducted in late December and January to exclude transitory migrating individuals. We did not capture individuals earlier in the season as prior to the second week of December Wilson's Warblers were not responsive to play-back, possibly because they had not yet established territories. Each bird captured was banded with Darvic color bands for later visual identification (Ralph et al. 1996). We recorded morphometric measurements of wing and tarsus length and body mass to obtain an index of body condition (Strong and Sherry 2001), calculated using body mass divided by wing length (Leary et al. 1999), where a higher index indicates better body condition.

Territory size

To obtain data on territory size we re-sighted and followed color-banded individuals, within four hours after sunrise, on two different occasions approximately two weeks apart during the winter (Marra and Holmes 2001). We measured the size of 63 territories: 23 in the conserved forest site (2011-2012 = 8 individuals, 2012-2013 = 8; 2013-2014 = 7 individuals); 20 territories in the moderate disturbance site (2011-2012 = 5, 2012-2013 = 7; 2013-2014 = 8 individuals); and 20 territories in the highly disturbed site (2011-2012 = 2, 2012-2013 = 8; 2013-2014 = 10 individuals). There were two territory estimates of the same individual in different winters: one in the moderately disturbed site, and one in the highly disturbed site. When a banded bird was re-sighted, we followed its movements for 10 mins (excluding time when the bird was perched), and recorded each new location with a GPS, considering a minimum of 5 georeferenced points for each individual (Marra and Holmes 2001). We calculated territory size using the Minimum Convex Polygon function in Hawth's tools (Beyer 2004) and the Layer attributes function in ArcGis 9.3 (ESRI 2008).

Statistical analysis

We evaluated normality of data using the Shapiro-Wilk test. The forest structure variables of mean tree height, mean shrub height, and tree basal area all presented a normal distribution, therefore we performed one-way ANOVA tests to compare these structural characteristics among the three sites with differing gradients of disturbance. Where a significant difference was found we applied Tukey post-hoc tests to determine which disturbance site was significantly different. However, we used Kruskall-Wallis ANOVA with Dunn post-hoc test to compare tree and shrub density among the three sites since these data sets did not have a normal distribution.

We analyzed point-count bird survey data using the Distance program (Thomas et al. 2010) to obtain Wilson's Warbler density estimates for each site, selecting the density model with lowest Akaike value, which in this case was the half-normal model. To determine whether density estimates were significantly different among sites, we compared 84% confidence intervals, assuming significant differences when confidence intervals did not overlap (Payton et al. 2003, MacGregor-Fors and Payton 2013). Density estimates based on 20 point-counts were compared among the three sites in the winters of 2012-2013 and 2013-2014. However, for the first winter of 2011-2012, we compared density estimates from just the conserved and moderate disturbance sites, since only 8 point-counts were conducted in the highly disturbed site during the first year, and this did not provide sufficient data for comparison.

We applied the Shapiro-Wilk test for normality on data for body condition and territory size. Data on body condition for the winters of 2011-2012 and 2012-2013 presented a normal distribution. Therefore for the first winter, we applied a two-sample *t*-test to compare body condition of birds between the conserved and moderately disturbed sites, as there was insufficient data to include the highly disturbed site in the comparison. However, for the second winter, we applied one-way ANOVA to compare body condition of birds among the three sites with differing degrees of forest disturbance. Body condition data for the third 2013-2014 winter, as well as that for all three winters combined, did not presented a normal distribution, thus we applied Kruskal-Wallis ANOVA to compare among the three sites. On combining the data from all three winters, we only included data for recaptured birds from the first winter they were captured, so as to preserve the assumption of independence for statistical tests.

Similarly, data on territory size for the first winter of 2011-2012 was normally distributed, therefore we performed a two-sample *t*-test to compare territory size of Wilson's Warblers between the conserved and moderately disturbed sites. However, territory size data for the 2012-2013 and 2013-2014 winters, and for all three winters combined, did not present a normal distribution, therefore we performed Kruskal-Wallis ANOVA to compare territory size among all three sites. For all statistical analyses we used alpha = 0.05, and descriptive statistics are presented as mean with standard deviation values.

Results

Habitat variation in forest structure

We found significant differences among forest sites in the structural variables of tree abundance ($H_{2,77} = 25.4$, $P<0.001$) and height ($F_{2,77} = 3.73$, $P = 0.028$), and shrub abundance ($H_{2,77} = 40.1$, $P<0.001$) and height ($F_{2,77} = 13.0$, $P<0.001$), although tree basal area did not differ among sites. Overall, the conserved forest site had a higher abundance of trees and shrubs, and these were taller than in the disturbed forest sites (Fig. 1). In particular, tree and shrub abundance were significantly higher in the conserved cloud forest site compared to the moderately disturbed (trees: $q= 2.53$, $P<0.05$; shrubs: $q=5.24$, $P<0.05$), and highly disturbed (trees: $q= 5.02$, $P<0.05$; shrubs: $q=5.54$, $P<0.05$) forest sites. Moreover the moderately disturbed site had significantly greater tree abundance than the highly disturbed site ($q= 2.46$, $P<0.05$). Trees were also significantly taller in the conserved forest compared to the moderately disturbed forest ($q= 3.79$, $P= 0.025$), and shrubs were significantly taller in the conserved site compared to both disturbed sites (Moderately disturbed: $q= 6.95$, $P< 0.001$; Highly disturbed: $q= 4.89$, $P< 0.003$).

Variation in bird density

During each of the three winters, density of Wilson's Warbler was highest in the conserved cloud forest site of Santuario Bosque Niebla (Fig. 2), with a mean 9.8 ± 1.6 ind/ha, which was more than double the density of Wilson's Warblers in the disturbed sites (Moderately disturbed: 4.3 ± 0.26 ind/ha; Highly disturbed: 4 ± 0.4 ind/ha).

Furthermore, density estimates at each site were consistent among years (Fig. 2). Comparison of the 84% confidence intervals demonstrated that in all three winters bird density was significantly higher in the conserved cloud forest site compared to disturbed sites (Fig. 2).

Variation in territory size

Overall, mean winter territory size of Wilson's Warbler in cloud forest was 766.2 ± 858.3 m^2 (n = 61 territories). Taking all three years together, birds in the conserved cloud forest site had smaller territories of 361.7 ± 228.2 m^2 (n = 23 birds), compared to a territory size of 1092.6 ± 1226.4 m^2 for 18 birds in the moderately disturbed site, and 890.2 ± 743.6 m^2 for 20 birds in the highly disturbed site. Furthermore, in each of the three winter seasons territory size was smaller in the conserved forest site compared to the disturbed forest sites (Fig. 3). We found a significant difference in territory size among sites for the third winter season ($H_{2,24}$ = 7.8, P = 0.021), and for all three seasons combined ($H_{2,58}$ = 8.41, P = 0.015). Dunn post-hoc analysis showed that in both cases birds in the conserved forest site had significantly smaller territories compared to birds in the highly disturbed forest site (2013-2014 winter: q = 2.79, $P < 0.05$; Combined winters: q=2.765, $P < 0.05$). Moreover, in the conserved forest territory sizes were small in each of the three winters, but birds in disturbed forest sites showed higher inter-annual variation in territory size (Fig. 3).

Body condition

Wilson's Warbler had an overall body condition index of 0.121 ± 0.005 for a total of 74 birds captured in cloud forest. Body condition of birds for all three winters combined did not differ significantly among cloud forest sites, where birds in the conserved forest site had mean body condition index of 0.120 ± 0.0049 (n = 30), compared to a mean body condition of 0.122 ± 0.0059 (n = 23) for birds in the moderately disturbed, and 0.121 ± 0.0051 (n = 21) for birds in the highly disturbed sites. When we analyzed body condition of birds for each winter season separately, we found significant differences only for the first winter of 2011-2012 between the conserved and moderate disturbance sites (t = 2.24, P = 0.042), as there was insufficient data to include the highly disturbed site in statistical analysis. In this first winter season, birds in the moderately disturbed forest had higher body condition compared to those in the conserved forest (Fig. 4). Finally, birds in conserved forest exhibited a relatively constant body condition index from one winter season to the next, whereas birds in the disturbed forest sites showed greater inter-annual fluctuation in body condition index (Fig. 4).

Discussion

We found that Wilson's Warblers in the conserved cloud forest site had higher bird density, smaller territory size, and inter-annually consistent body condition, suggesting that the conserved forest site represents higher quality winter habitat for the species. The conserved forest site also had greater abundance of taller trees and shrubs than the disturbed forest sites. Therefore, mature, conserved forest may have greater structural complexity able to hold a larger number of birds, with territorial individuals able to meet their resource requirements within a smaller defended area than birds in disturbed forests. A high quality habitat is considered to have sufficient resources to support a higher population size than a low quality habitat (Gilroy and Sutherland 2007). Nevertheless, density estimation alone may not be a good indicator of habitat quality, and needs to be accompanied with the evaluation of other variables (van Horne 1983; Vickery et al. 1992; Marra and Holmes 2001). Thus, the fact that Wilson's Warblers also have smaller territories in the conserved forest, and that all three variables of density, territory size, and body condition are consistent among winter seasons in the conserved forest site, strengthens the conclusion that this represents higher quality habitat for migrating Wilson's Warblers.

Wilson's Warbler appears able to breed in both disturbed and undisturbed habitats (Hejl et al. 1995; Desrochers et al. 2012). During migration however, forest habitats may be more suitable stopover sites for the species, as forest sites with tall trees and a mix of shrub enabled birds to gain body mass at a higher rate and spend less time in stopovers compared to agricultural fields and edge habitats (Yong et al. 1998). This is supported by our findings for the winter season, where conserved cloud forest, with more abundant and taller shrubs and trees, may provide homogenous and consistent habitat conditions among years, enabling migrating birds to maintain similar behavior and condition through time, as indicated by the relative constancy of bird density, territory size, and body condition among years at the conserved forest site.

Wilson's Warbler territory size in cloud forest was smaller than all previous territory estimates for the species. Our overall territory size estimate of 737 m^2 was one sixth of the territory size reported for Wilson's Warbler during the winter in the rainforest of Veracruz (Rappole and Warner 1980). This was also ~27 times smaller than territory sizes reported for Wilson's Warbler at summer breeding grounds in North America (Stewart 1973; Stewart et al. 1977; Eckhardt 1979), which can be as large as 20,000 m^2 (Stewart et al. 1977). This pattern of smaller winter territories compared to breeding territories is shared by other insectivorous warblers such as the Hooded Warbler, *Setophaga citrina* (Howlett and Stutchbury 1997; Rappole and Warner 1980), and American Redstart, *Setophaga ruticilla* (Sturm 1945; Ficken 1962; Sherry and Holmes 1989, 1997). Coincidently, for migratory birds during the winter, larger territories have been reported in disturbed habitats (pastures and hedgerows), added to which a high proportion of birds are non-territorial (Rappole and Warner 1980; Rappole and Morton 1985).

Territories as small as those maintained by Wilson's Warblers in the cloud forest of Veracruz have also been reported for the Yellow Warbler (*Setophaga petechia*) in Chiapas, Mexico, where individuals defend the richest arthropod habitat (several trees) within a pasture matrix (Greenberg and Salgado-Ortiz 1994). Therefore, the overall small territory size recorded for Wilson's Warblers in our study suggests that cloud forest may be a resource rich wintering habitat. Cloud forest may present benign microclimatic conditions for Wilson's Warblers since humid habitats with increased rainfall have greater arthropod abundance, and are better habitats for primarily insectivorous migratory birds (Latta and Faaborg 2002; Studds and Marra 2005; Brown and Sherry 2006; Studds and Marra 2007; Smith et al. 2010). Cloud forest has high levels of precipitation, similar to other wet-forest habitats, although even rainforests have been reported to have lower arthropod abundance than cloud forest (Townsend et al. 2012). Moreover humid habitats have been linked to improved body condition of another Neotropical migratory warbler, *Setophaga ruticilla* (Marra et al. 1998; Marra and Holmes 2001).

Body condition of Wilson's Warblers was similar among sites, although there was higher inter-annual fluctuation in body condition of birds in the disturbed forest sites. Birds have alternative strategies to compensate for resource differences, such as modifying their diet through foraging plasticity (Martins et al. 2013), storing more fat in habitat with few or less constant resources (Strong and Sherry 2000), and defending a larger territory. The significantly larger territory sizes of Wilson's Warblers in disturbed forest sites suggests that they adjust territory size as a strategy to compensate for resource differences between conserved and disturbed forests. Furthermore, the fact that Wilson's Warblers maintain territories in disturbed cloud forest shows that such disturbed habitats may still be beneficial, since defending territories implies trade-offs by making the individual more conspicuous to predators (Campos et al. 2009), and leading to aggressive behavior with high energy costs in the restriction of time spent foraging (Cresswell 2008); risks that birds would not take unless there was a worthwhile benefit. Territoriality has been shown to be a strategy enabling access to high quality habitats, for another migratory insectivorous warbler, the

Ovenbird (*Seiurus aurocapillus*), where territorial birds have higher body mass with lower foraging rates when compared to floaters (Kresnik and Stutchbury 2014).

The low variation in body condition and territory size among Wilson's Warbler individuals in the conserved forest suggests that this is the most homogenous habitat of the three sites. The greater area of forest cover in the large conserved forest fragment may lead to greater food resource availability, since higher insect abundance has been found in continuous forest compared to fragmented forests (Ruiz-Guerra et al. 2012). Furthermore, the inter-annually consistent territory size and body condition of birds in the conserved forest indicates resource stability, similar to that found in other evergreen forests when compared to drier habitats (Brown and Sherry 2006; Smith et al. 2010). This inter-annual resource stability could be an additional benefit for migratory birds making conserved forest conditions more predictable from year to year compared to disturbed forests, and this predictability could ultimately be reflected in individual overwintering survivorship. The high inter-annual variability in territory size and body condition of Wilson's Warblers in disturbed forests suggest that forest habitats subject to human disturbance are less stable over time, which may represent a drawback when selecting winter territories. Greater resource stability in mature, conserved cloud forest would make this a more reliable habitat over the years for wintering Wilson's Warblers, increasing their chances of survival, and the likelihood that they will maintain good body condition, essential for an early return to breeding grounds and increasing fitness (Marra et al. 1998). By comparison, variable conditions in disturbed forest fragments could work as an ecological trap, preventing birds from seeking better territories when conditions appear to be good, which in subsequent years may be radically different (Ekroos et al. 2012).

Our results are of greater relevance considering that we found differences in Wilson's Warbler winter ecology within the same forest type, but under differing levels of disturbance. Differences in winter ecology have generally been determined between distinct and more contrasting habitat types (Marra et al. 1998; Latta and Faaborg 2002; Sherry and Holmes 1996; Saino et al. 2004), where variations are more likely to occur. However, our results demonstrate that even changes in area and structure of the same habitat type could significantly affect wintering performance of migratory birds, and the carry-over effects could be different for individuals wintering in different sites within the same habitat.

Taken together our findings suggest that mature, conserved cloud forest represents a high quality wintering habitat for Wilson's Warbler, and this habitat condition could also benefit other migratory birds that have similar ecological requirements. Our population-level analysis of bird density demonstrated that conserved forest was able to hold a greater number of territorial and non-territorial birds. On the other hand, individual evaluation of territory size and body condition suggests that territorial birds inhabiting disturbed forest meet their requirements to maintain body condition by expanding territory size, since territoriality reduces intra-specific competition (Odum and Kuenzler 1955) and provides exclusive access to food resources (Parrish and Sherry 1994; Sogge et al. 2007). However, the high variability in territory size and body condition of birds in disturbed forests among years suggests that the effectiveness of adjusting territory size may vary from year to year.

To properly direct conservation efforts it is important to understand the effects of wintering habitat on the behavior and population traits of migratory birds, particularly since wintering habitat has important carry-over effects on breeding success (Marra et al. 1998; Norris et al. 2004; Reudink et al. 2009). Knowledge of habitat use by Neotropical migratory warblers during the winter helps to reveal features of the habitat that could be driving population declines. We stress the importance of actively protecting remnants of mature cloud forest, and second-growth forest that can be restored, which bird density, territory size and body condition all indicate are better quality habitats for Wilson's Warblers. Future studies addressing Wilson's Warbler wintering ecology in different habitats would help to understand the importance of each habitat in the species wintering dynamics and its entire life cycle. The results of our study confirm that even when birds are able to offset resource limitations through physiological and behavioral plasticity (Weber and Hedenström 2001; Pierce and McWilliams 2005), disturbed habitats are not ideal for migratory birds, and we still do not know the implications for trade-offs when balancing resource shortages. Migratory birds undergo seasonal changes in needs and behavioral traits, and only by understanding the way in which they utilize available habitats will we be able to propose the most appropriate strategies to preserve, and as a more ambitious goal, possibly to improve the status of wild populations.

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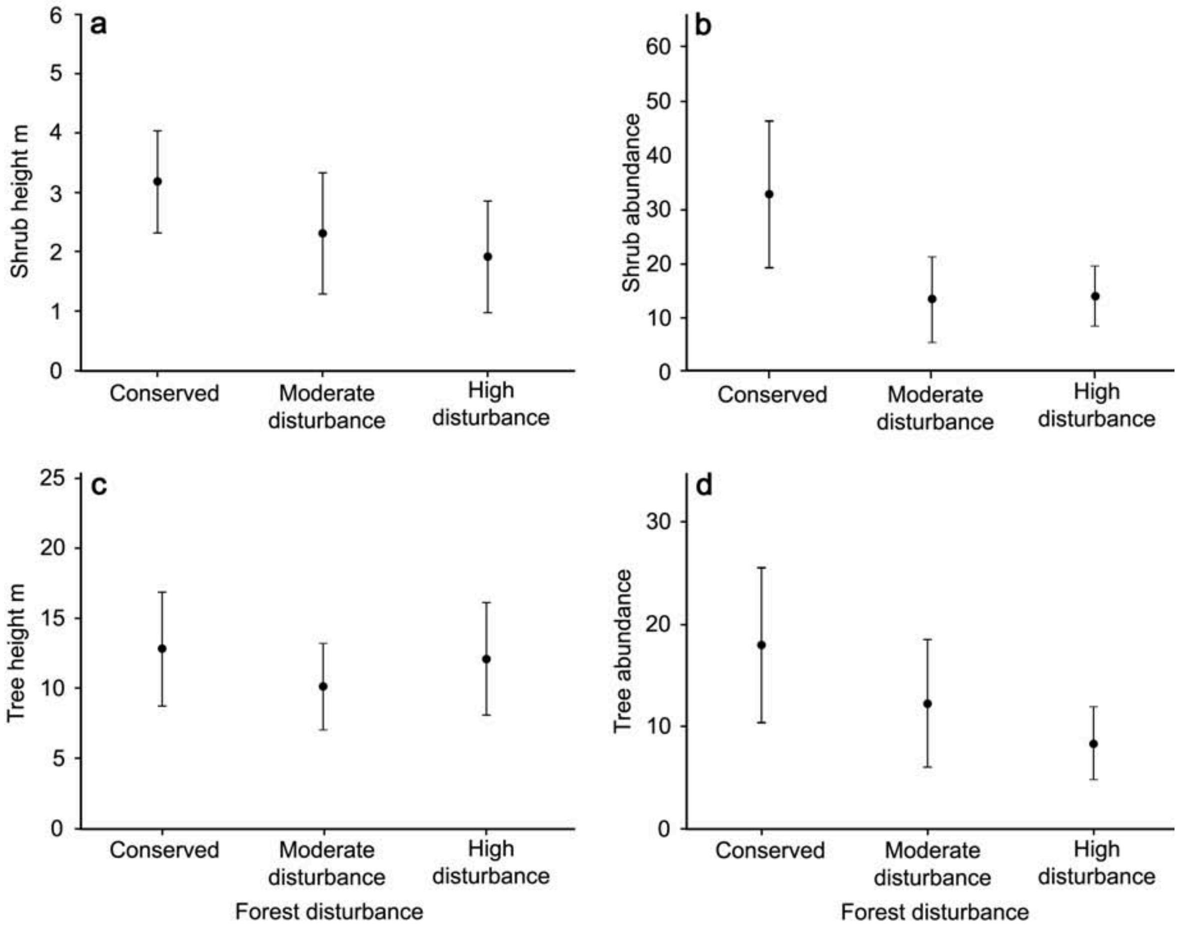
Figure captions

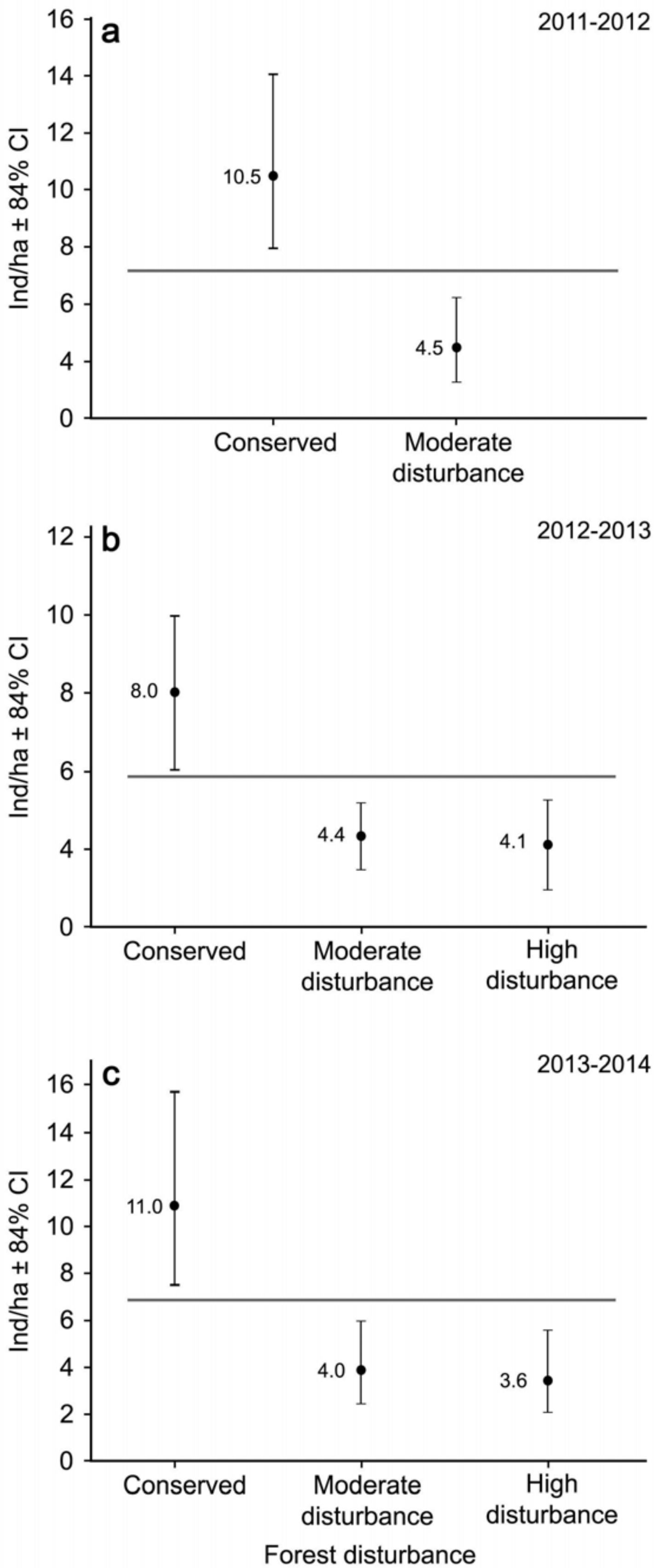
Fig. 1 Mean (± SD) vegetation structure of **a** shrub height, **b** shrub abundance, **c** tree height, and **d** tree abundance within Wilson's Warbler territories in three cloud forest sites with differing degrees of disturbance

Fig. 2 Density estimates with 84% confidence intervals for Wilson's Warblers at three cloud forest sites with different degrees of disturbance, in three consecutive winters **a** 2011-2012, **b** 2012-2013, and **c** 2013-2014, based on 20 point-counts per site. The black line denotes a significant difference among sites where confidence intervals do not overlap

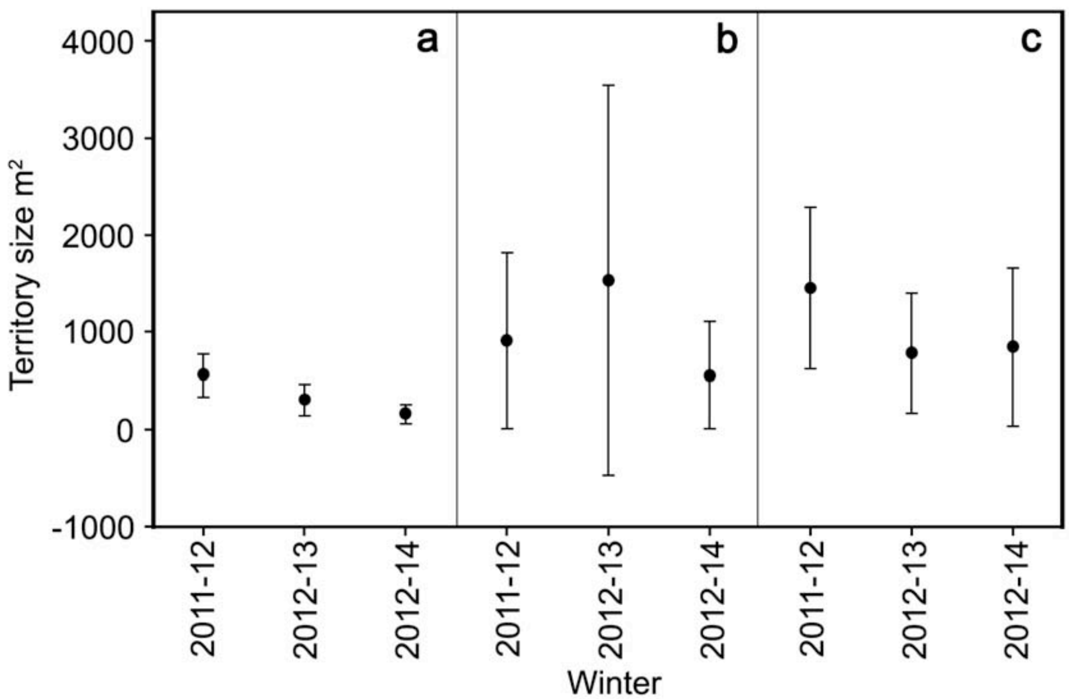
Fig. 3 Mean (±SE) territory size of Wilson's Warblers in three cloud forest sites with differing degrees of disturbance (**a** conserved, **b** moderately disturbed**, c** highly disturbed**)** over three consecutive winters (2011-2012, 2012-2013, 2013-2014)

Fig. 4 Mean body condition (± SD) of territorial Wilson's Warblers at three cloud forest sites with different degrees of disturbance (**a** conserved, **b** moderately disturbed**, c** highly disturbed) in three consecutive winters (2011-2012, 2012-2013, 2013-2014)

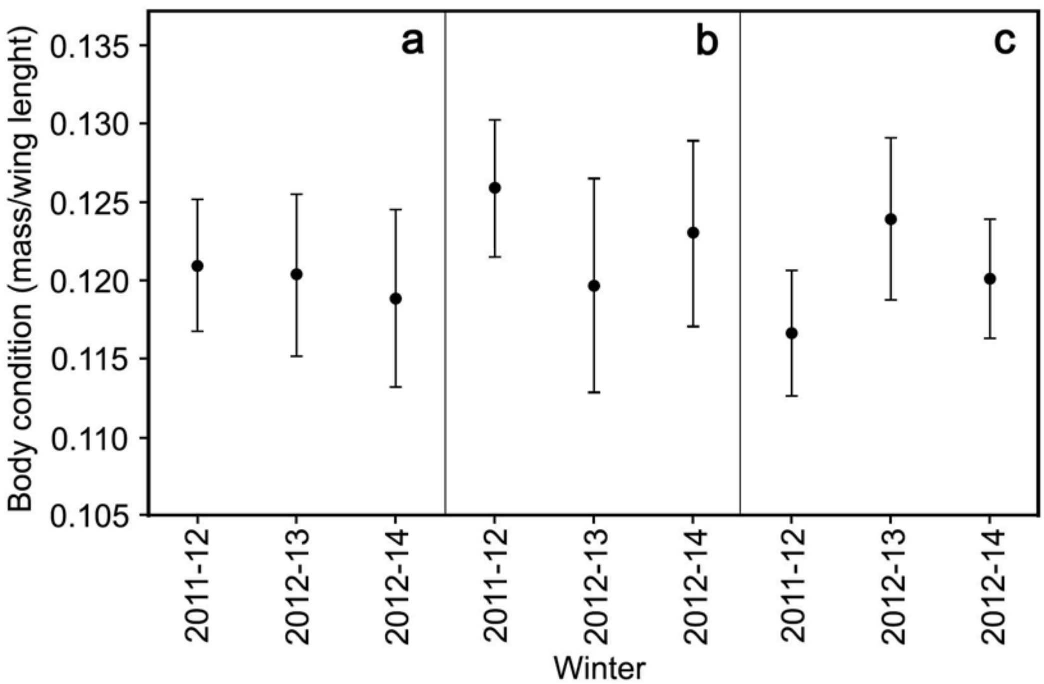

a
Shrub height m
0
1
2
3
4
5
6
b
Shrub abundance
0
10
20
30
40
50
60
c
Tree height m
0
5
10
15
20
25
d
Tree abundance
0
10
20
30
Conserved
Moderate disturbance
High disturbance
Forest disturbance



a
2011-2012
Ind/ha ± 84% CI
16
14
12
10
8
6
4
0
10.5
4.5
Conserved
Moderate disturbance
b
2012-2013
Ind/ha ± 84% CI
12
10
8
6
4
0
8.0
4.4
4.1
Conserved
Moderate disturbance
High disturbance
c
2013-2014
Ind/ha ± 84% CI
16
14
12
10
8
6
4
2
0
11.0
4.0
3.6
Conserved
Moderate disturbance
High disturbance
Forest disturbance



a
b
c
4000
3000
2000
1000
0
-1000
Territory size m²
2011-12
2012-13
2012-14
2011-12
2012-13
2012-14
2011-12
2012-13
2012-14
Winter



Body condition (mass/wing lenght)
0.135
0.130
0.125
0.120
0.115
0.110
0.105
a
b
c
2011-12
2012-13
2012-14
2011-12
2012-13
2012-14
2011-12
2012-13
2012-14
Winter

A TWO-WAY STREET: CARRY OVER EFFECTS OF SUMMER BODY CONDITION ON WINTER TERRITORY SELECTION OF A NEOTROPICAL MIGRATORY WARBLER

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ABSTRACT

Winter habitat quality has been shown to influence body condition of migratory birds, and fitness in summer breeding grounds. However, little is known of how breeding condition may influence wintering site selection. We explored the relationship between summer breeding body condition of the Neotropical migratory Wilson's Warbler, and wintering site vegetation structure, food abundance, territory size and winter body condition. We color-banded 68 birds during the winters of 2011 to 2014 in cloud forest fragments of central Veracruz, Mexico. For each banded Wilson's Warbler we measured body mass and wing length to obtain an index of winter body condition, and determined winter territory size by re-sighting and response to play-back of marked individuals. Within each Wilson's Warbler territory we evaluated habitat structure (tree basal area, shrub and tree abundance and height) and food abundance (arthropods consumed in the diet). We also collected feathers from each banded Wilson's Warbler to determine summer breeding body condition by intensity of yellow pigmentation on tail feathers grown in the breeding grounds, since carotenoids used to build yellow in feathers are obtained through the diet, and therefore reflect body condition. We also analyzed tail feather macrostructure (feather length, width, and apex width) and microstructure (barb barbule length and barbule width) as summer breeding body condition, given that aerodynamic properties and feather durability depend on physical characteristics. Our results demonstrated that Wilson's Warblers with the highest summer body condition (longest barbules from feather microstructure) had winter territories with high shrub abundance. Food abundance in winter territories was positively related mainly to tree abundance, but also to shrub abundance, and birds maintained smaller territories when these had high shrub abundance. Hence, warblers with higher summer breeding condition tended to have winter territories with habitat structure of high tree and shrub abundance, characteristic of conserved forests, where there may be higher food abundance, and they could maintain smaller winter territories. Our study demonstrates that winter-summer carry-over effects of body condition of migratory birds, may work both ways, and highlights the importance of maintained conserved forests as high quality habitats for migratory birds.

Keywords: arthropod abundance, body condition, cloud forest, feather microstructure, habitat structure, Mexico, territory size, Wilson’s Warbler, wintering ecology.

INTRODUCTION

Carry-over effects of body condition in one season influencing opportunities in the subsequent season are particularly relevant for migratory bird species that travel thousands of kilometers to change location between summer and winter, sometimes also changing ecological preferences, such as habitat (Hahn et al. 2013). To adapt to this drastic change of conditions among seasons, birds have different behavioral and physiological strategies that are limited by the species' plasticity, such as compensating for low body condition by spending less energy on feather coloration (Norris et al. 2004), or by increasing the rate of fattening during migration (Clausen et al. 2015).

Plasticity of behavior allows migratory birds to balance habitat resource variations such as food abundance, not only by employing strategies of territoriality or vagrancy, but also by allowing adjustments in territory size. Small territories are established in areas with high food resource abundance, while territories may be larger in areas with lower food resources (Verner 1977, Myers et al. 1979), therefore winter territory size could indicate habitat quality.

Vegetation structure is one of the main cues that birds utilize to rapidly assess habitat quality when they first arrive to an area after migration (Kotliar and Wiens 1990, Xu et al. 2006). In general, Neotropical migratory warblers have shown high abundance in wintering forest habitats, possibly due to higher arthropod abundance in forests as these tend to be more humid habitats compared to open habitats (Latta and Faaborg 2002, Studds and Marra 2005, 2007, Brown and Sherry 2006, Smith et al. 2010). Moreover, the more complex vegetation structure of forests may influence accessibility of prey, and foraging strategies, independent of prey abundance (Poulin and Lefebvre 1997, Whelan 2001, van Oosten 2014).

Over the last two decades, the study of Neotropical migratory birds has acquired greater relevance given the accelerated rate of decline determined for this group (Robbins et al. 1989, Askins et al. 1990, Ballard et al. 2003, Sauer et al. 2014). Population decline has been attributed mainly to loss and modification of habitat in the wintering grounds (Robbins et al. 1989, Askins et al. 1990, Rappole and McDonald 1994). Therefore, studies evaluating carry-over effects, whereby body condition acquired in one season may influence opportunities and performance in the subsequent season, could help to elucidate the key factors affecting bird populations, and influencing the decline of Neotropical migrants. Winter habitat quality has been shown to influence body condition and fitness of migratory birds, as individuals wintering in higher quality habitats have higher body condition, arrive earlier to breeding grounds, and have increased breeding opportunities (Marra et al. 1998, Reudink et al. 2008). Conversely, the condition of birds after summer breeding opportunities could also affect their performance in the subsequent winter season, and a decade ago Hill (2004) called attention to the importance of potential carry-over effects from summer to winter. However, almost nothing is known of how summer breeding condition may influence winter migration site selection.

We assessed carry-over effects of summer body condition on winter opportunities for Wilson's Warbler (*Cardellina pusilla*) in cloud forest fragments of central Veracruz, Mexico. This Neotropical migratory species has shown an overall population decline of 2.1% annually since 1966 (Desrochers 2012, Sauer et al. 2014). The species is commonly considered a habitat generalist (Hutto 1981, Berlanga et al. 2010), but demonstrates improved condition in forested stop-over sites during migration (Yong et al. 2008), and conserved forest may be more suitable habitat for the species during the winter (Ruiz-Sánchez et al. submit.). Furthermore, Wilson's Warbler exhibits winter territoriality, particularly in forest habitats where it is generally abundant

(Hutto 1981, Lynch 1989). If there are carry-over effects of summer body condition on winter opportunities, then we expected that individuals with better summer body condition would establish winter territories in conserved cloud forest, with higher food abundance, enabling them to maintain smaller territories, and in turn exhibiting better winter body condition.

METHODS

Study area

The study was conducted in cloud forest fragments of central Veracruz, Mexico, which is considered an Important Bird Area (Arizmendi and Marquez Valdelamar 2000). We selected three sampling sites separated by no more than 11 km, and within an altitudinal range of 1320-1690 m asl: i) the Santuario de Bosque de Niebla Francisco Javier Clavijero, a protected forest reserve (19º30’13.369” N, 96º56’5.083” W); ii) El Tejar Garnica (19º31’12.612” N, 96º53’32.05” W), a smaller protected forest remnant in the outskirts of the capital city of Xalapa; and iii) Rancho El Trébol (19º35’43’’ N, 96º58’4’’ W), an unprotected farm with small cloud forest fragments within an agricultural matrix. The region has a temperate-humid climate with mean temperature of 18°C, and year-round rainfall of 1500-2000 mm annually (Williams-Linera et al. 2013).

Bird capture and banding

We aimed to study exclusively territorial birds in the wintering ground, therefore we used mist-netting with play-back to attract targeted birds to the nets (Johnson et al. 1981). We captured territorial birds during three winter seasons 2011-12, 2012-13 and 2013-14, from late December to January to exclude transitory migrating individuals, and because birds did not demonstrate territorial response to play-back prior to the second week of December (Ruiz-Sánchez et al. in revision). We set up from two to four mist-nets of 12 m length and 32 mm mesh size within each Wilson's Warbler territory. We captured 68 individuals of Wilson's Warbler, which were marked with Darvic colored leg-bands for later individual visual identification, re-sighting, and territory mapping.

Body condition

Each captured Wilson's Warbler individual was measured to obtained body mass and wing-length. We then calculated winter body condition index as body mass divided by wing length (Strong and Sherry 2001, Leary et al. 1999), where a higher body mass/wing length ratio is considered to be indicative of better body condition. We also plucked one tail feather (R1 right) from each captured Wilson's warbler, which were stored in individual envelopes for later evaluation to assess summer body condition, since these tail feathers are grown over the summer at breeding grounds (Pyle 1997).

Feather coloration

Wilson's Warbler is easily recognizable by its olivegreen upperparts and yellow underparts and forehead (Weicker and Winker 2002), however mechanisms responsible for its coloration are poorly known. Feather coloration is produced by the differential absorption of light by pigments, carotenoids and melanins (pigmentary colours) or by the interaction of light waves with specialized microstructures of feathers (structural colours) (Shawkey et al. 2005). Carotenoids typically give a red, orange and yellow hue to animals (Hill and MacGraw 2006). It is well established that carotenoid deposition in feathers is dependent on food intake and carotenoid access, therefore a conspicuous carotenoid coloration would be characteristic of birds able to forage more efficiently, thereby serving as an honest signal of body condition (Hill 1999, Møller et al. 2000, Saks et al. 2003). We evaluated the Wilson,s Warbel coloration through of a yellow line that appears in a plucked tail feather taken of each individual.

We used a digital camera (Sony Cyber-Shot DSC-W570) with 16.1 pixel resolution to photograph tail feathers. To be photographed, each feather was placed in the same position against a white background so that the entire yellow strip on the tail feather would be visible in photographs, and the camera was placed at a distance of 20 cm, with an angle of 90º between the lens and the surface of the feather. The same color standard scale was settled in each photograph to standardize the light condition in the subsequent analysis color. We took four measurements of the red, green, and blue color values (RGB values) along the yellow strip of the feather from digital images using the color sampler tool set to a 31X31 pixel sampling with Adobe Photoshop CS6. We then averaged the four measurements to produce a single RGB value for each individual feather, and these values were converted to hue, saturation and brightness (HSB values) by the algorithm described in Foley and Van Dam (1984).

Feather structure

We determined physical feather characteristics at a macroscopic and microscopic level, given that aerodynamic properties, durability, and even feather coloration depend on structural features such as barb density, length and weight (Shawkey and Hill 2005). Feather structure could also reflect body condition since alimentary stress is negatively related to the macroscopic feature of total feather weight (Murphy et al. 1988), and to microscopic features of barb and barbule density (Hargitai et al. 2014). Therefore, we measured four macroscopic tail characteristics i) feather length, the distance from the quill base to the distal tip of the feather; ii) Maximum feather width; iii) Apex width, using a Mitutoyo digital caliper to the nearest 0.01 mm.

To determine microscopic features, we mounted the feathers over carbon discs and used a Scanning electron microscope (Model JEOL JSM-5410LV) at 25 kV voltage acceleration to take pictures at 15X, 150X and 350X magnification. All feather measurements were taken in the first centimeter starting at the apex of the feather. We measured seven microscopic characteristics from the images, using the Image- Pro Plus software: i) barb length, length of the tenth barb starting from the apex on the right side of the raquis, iii) average barbule length, from any five barbules from the right side of the raquis and iii) average barbule width, from the five barbules selected to measure barbule length.

Winter territory size

We searched for each color-banded bird on two different occasions, separated by approximately two weeks, and followed birds when they were re-sighted. We conducted re-sighting and territory mapping of marked birds within four hours after sunrise (Marra and Holmes 2001), and followed the movements of each banded bird for at least 10 mins (excluding the time birds spent perched, resting, or grooming), during which time we recorded each change in location with a GPS. We considered a minimum of 5 georeferenced points to define each individual territory (Marra and Holmes 2001). Territory limits were corroborated through response to play-backs. We were able to measure 64 territories as 4 marked birds were not re-sighted on two occasions after capture.

Vegetation structure

In each Wilson's Warbler territory we established one 25 m diameter circular plot (Blake and Hoppes 1986) within which we measured five variables of habitat structure: a) tree basal areas, b) shrub abundance and height, c) and tree abundance and height. These variables were chosen given that woody vegetation is one of the first to be altered or removed due to human disturbance, and because habitat suitability seems to be related to tree and shrub forest composition (Hejl et al. 1995, Yong et al. 1998, Graham and Blake 2001, Ruiz-Sánchez et al. in revision). Within each plot we counted all trees and shrubs to estimate abundance, and measured their height using a clinometer (Suunto PM-5). We estimated tree basal area by variable radius plot sampling using an angle gauge (JIM-GEM® Cruz-All) with an English basal area factor of five, where we multiplied by 5 the total number of tree hits with the angle-gauge.

Arthropod abundance

Focal foraging observations performed prior to this study showed that >85% of foraging maneuvers by Wilson's Warblers were performed from a substrate and that aerial attacks were sporadic (Ruiz-Sanchez unpubl. data). Thus, we opted for the use of a sweep-net to sample arthropods that may be consumed by Wilson's Warbler. We swept the vegetation from the ground up to 2 m high, in four transects of 12m length, along and across the net lane were each bird was caught (Blake and Hoppes 1986). Arthropods were preserved in containers with 70% ethanol, prior to identification.

We determined arthropods in the diet of Wilson's Warbler based on information from the literature, and from 30 samples of droppings excreted by captured birds at our sites. We analyzed each dropping sample under the stereo microscope (Celestron 44202) to separate out and identify arthropod remains to Order level. Only the arthropod Orders found in dropping samples were considered for the evaluation of food abundance in the sweep-net samples obtained at capture sites. Furthermore, only prey of less than 0.5 mm length were considered as potential food items, since prey greater than 0.5 mm are less likely to be consumed by Wilson's Warbler (Poulin and Lefebvre 1997, Hagar et al. 2007, ARS pers. obs). We used the weighted abundance index proposed by Poulin and Lefebvre (1997) that avoids potential bias in food abundance estimation when several arthropod Orders are abundant, although they may not be the Orders most consumed by Wilson's Warblers. The formula is as follows:

$$\text{Weighted abundance index} = \sum_{j=1}^{n} p_i \frac{x_{ij}}{y_i}$$

Thus the abundance of each arthropod taxon <0.5 mm (x_{ij}) was divided by the number of arthropods from that Order collected in the whole sample (y_i), and multiplied by the proportion of each arthropod group in the bird's diet (p_i) as a weighting factor. In this way, the sum of weighted abundance indices for each Order reached high values when several Orders consumed by Wilson's Warbler were abundant in the sample.

Statistical analysis

We used three independent Principal Component Analysis procedures on a) feather color, b) macro structure, and c) micro-structure variables, to reduce the number of dimensions for statistical analysis to three summer body condition indexes. In all three cases, PC1 had an eigenvalue higher than 64%. In order to explore the effect of summer body condition on the characteristics of the wintering territories, we performed regression analysis. We used the first principal component from feather color, macro structure and micro structure as independent variables and winter territory characteristics as dependent variables (tree abundance, shrub abundance, tree height, shrub height, tree basal area, food abundance and territory size). We also explored the effect of winter territory characteristics on winter body condition (body mass/wing length). Additionally we performed regression analysis to assess if there was an effect of any of the vegetation structure characteristics or food abundance on the size of the territory. We used an alpha value = 0.05 in all cases.

We also performed regression tree analysis in the R Package TREE (Ripley 2014), to explore potentially linear or non-linear relationships (De'ath and Fabricius 2000) and determine hierarchical thresholds in the relationship between variables for summer body condition (feather coloration and structure) with winter territory traits (vegetation structure, food abundance, and territory size), as well as winter body condition with winter territory traits. Furthermore, we applied regression trees to explore relationships within winter territory traits of vegetation structure with food abundance and territory size. Regression trees were fitted with all age/sex classes pooled and were pruned using the function prune with software- predefined cross-validation parameters and a user-predefined deviance of 0.001. All analyses were conducted in R version 3.1 (R Core Team 2014).

RESULTS

Summer body condition and winter territory traits

Feather microstructure measurements were condensed into one principal component, which explained >90% of the variation in our data, the variable with more weight on PC1 was average barbule length. Feather macrostructure measurements were condensed into one principal component, which explained 83% of the variation in our data, the variables with more weight on PC1 were total length and width. Finally, color composition was condensed into one principal component, which explained >90% of the variation.

The regression analysis showed a positive relationship between PC1 of feather microstructure and winter territory shrub abundance ($r^2 = 0.25$, $df= 47$, F=14.967, P <0.001, Figure 1). We found that Wilson’s Warbler with highest summer body condition were located in territories with higher shrub abundance.

The regression tree showed that birds with the lowest summer body condition (feather microstructure) were caught in territories with a shrub abundance of <9 shrubs per plot, and these were grouped separately from birds in other territories with more shrubs (Figure 2). Furthermore, the regression tree demonstrated a secondary division where birds in territories with higher shrub abundance (> 26 shrubs per plot) had the highest summer body condition (Figure 2). Almost 70% of the territories were located in areas with more than nine shrubs.

Neither feather macrostructure nor feather coloration showed any relationship to winter territory characteristics. Also, we found no significative relationships among any of the summer body condition measurements and territory size or food abundance.

Relationships among winter territory traits

Regression tree analysis showed that food abundance in winter territories was positively related, primarily, to shrub abundance and also to tree abundance. Food abundance was higher in territories with >18 trees per sample plot, and these territories were grouped separately based on their food resource abundance (Figure 3). Highest food abundance was predicted for territories with both high tree and shrub abundance (>18 trees, >24 shrubs), and food abundance in these territories was double that predicted for territories with less than 18 trees, but with high shrub abundance (Figure 3). Lowest food abundance was predicted for territories with less than 6 trees, with fewer than 20% of territories falling into this category (Figure 3).

Winter territory size was also significantly related to tree and shrub abundance (r^2=0.26, F_{41}=13.48, P=0.001). Territories varied from 106 m^2 to 2270 m^2, and was negatively related to tree and shrub abundance, where birds maintained smaller territories in forests with higher tree and shrub abundance (Figure 4). Regression tree analysis showed that territory size was mainly related to shrub abundance, where birds maintained the largest territories in sites with low shrub abundance (<15.5 shrubs) forming a separate group to territory sizes predicted for sites with high shrub abundance (Figure 4). The smallest territories where predicted for birds in areas with a combination of high shrub and tree abundance (>15.5 shrubs + >7.5 trees), and birds in these areas maintained territories less than a third the size of birds in areas of low shrub abundance (Figure 4).

We found no relationship between food abundance and territory size. We also found no relationship between winter body condition and vegetation structure, food abundance, or territory size.

DISCUSSION

Our study reveals carry-over effects from summer to winter for migratory birds. Shrub abundance was the main variable influencing winter territory size and food abundance. Furthermore, winter territories were smaller and food abundance higher in areas with high tree and shrub abundance, characteristic of conserved forest. Therefore, summer body condition (feather microstructure) may determine wintering opportunities, particularly by influencing winter territory selection. Individuals that maintained higher body condition during the summer established winter territories in forested areas with high shrub abundance, which favored higher food abundance, and smaller winter territory sizes. Previous studies have demonstrated carry-over effects of winter body condition on summer breeding opportunities for Neotropical migratory birds (Marra et al. 1998, Marra and Holmes 2001), but this is the first study to demonstrate carry-over effects from summer to winter, and emphasizes the relevance of habitat quality in every season of a bird's lifecycle.

Our results showed that birds with lower body condition, particularly shorter feather barbules, during the summer, occupied winter territories with lower shrub abundance that may be suboptimal territories given that low shrub abundance was the main factor predicting low food abundance and large winter territory size. For birds with lower summer body condition, this could potentially lead to further disadvantages during the winter season or even affect subsequent summer breeding opportunities if individuals are not able to compensate for disadvantages during the winter or in spring migration. Clausen et al. (2015) found that poor body condition of the migratory Pink footed Goose (*Anser brachyrhynchus*) derived from harsh winter weather is traceable during the spring, but individuals were able to compensate body condition during spring migration and this did not persist to influence breeding opportunities. It is unknown whether Neotropical warblers may have similar abilities to balance adverse conditions encountered in summer breeding grounds or winter migration sites; however, if this were the case we would not expect to find a relationship between summer body condition and winter habitat quality. Similarly, carry-over effects of winter body condition influencing summer breeding opportunities have also been frequently reported (Marra et al. 1998, Marra and Holmes 2001, Saino et al. 2004).

The relationship of high shrub abundance in the first place, but also of high tree abundance with smaller winter territories in our study, demonstrates that these two vegetation structure traits were the most influential territory conditions determining the size of the wintering defended area. This coincides with the previous knowledge of Wilson's Warbler affinity to shrub habitats during the breeding season (Finch 1989, Douglas et al. 1992), and to deciduous shrub and riparian shrub understory during migration (Manuwal and Huff 1987). Wilson's Warbler is able to forage from ground level up to 17m high when tall trees are present (Stewart 1973, Hutto 1981); however, it usually forages between 0.8m and 2.4m in the shrub and understory layers (Morrison 1981). The species has been found to be more abundant where deciduous tree and shrub cover are higher (Morrison 1981, Morrison and Meslow 1983, Kessel 1998), and even when during the winter season, the species inhabits a more diverse range of habitats, it still is more abundant in forests (Hutto 1981, Lynch 1989). Wilson's Warbler density is particularly higher in conserved cloud forest were shrub and tree abundance are higher and where territories are also smaller, suggesting higher density of territorial birds (Ruiz-Sánchez et al. submit.). It has been suggested that high bird abundance, a population trait that can reflect habitat quality (Vickery 1992, Greenberg 1992, Lefebvre and Poulin 1996), is associated to high arthropod availability and to the complexity of understory and mid story vegetation structure (Moorman et al. 2012).

Although not significant in our regression analysis, the relationship between shrub and tree abundance with territory size indicate an indirect relationship between arthropod abundance and the territory size of Wilson's Warbler, given that territory size is modified in response to resource abundance, where small territories are stablished in areas with high food resources, and large territories are stablished in areas with lower food resources (Verner 1977, Myers et al.

1979).This suggest that high shrub and tree abundance are related to high food resources in the cloud forest. Moreover tree abundance is the main trait separating high food abundance from low food abundance territories; however, in low tree abundance territories, food resources could not be low in the presence of high shrub abundance. We would expect forest areas, that combined both a dense woody vegetation and high food abundance, to be occupied by birds with high summer body condition (longer feather barbules) when establishing their territories. This is true for some individuals in our study. However, for those that do not match this pattern, we suggest they could have encountered unfavorable conditions during migration, such as high speed winds and rain, that could have diminished their condition (Drake et al. 2014a), possibly making them less competitive to select territories or even delay their arrival to wintering grounds. The time birds spend on stopovers depends on the site ecological conditions and on opportunities for refueling to continue migration (Fransson 1998). These situations would put birds in disadvantage against other conspecifics to select wintering habitat and territories.

Only 26% of the variation in territory size was explained by this relationship with shrub abundance, therefore other habitat traits occurring at a different scale, may play a role in influencing territory size, such as landscape features of forest patch size and adjacent habitat matrix (Kotliar and Wiens 1990, Xu et al. 2006). At the same time, long migratory distances could dampen carry over effects, as it has been shown by the study of the influence of winter habitat use, on breeding phenology and productivity of Yellow Warblers (*Setophaga petechia*) (Drake et al. 2014b). It has been suggested that Wilson's Warbler is a complex that comprises two cryptic species which genetics and ecological niche are different, and both of these have been registered in the center of Veracruz (Irwing et al. 2011, Ruiz-Sánchez et al. 2015), therefore birds in this study could have different breeding origins and variation in migration distance along with differences in ecological needs could account for some of the weakness of the relationship, found in this study, between cloud forest traits (vegetation and food) and summer body condition (feather microstructure).

We did not find any relationship between feather coloration and winter territory characteristics (vegetation structure, food abundance or territory size). This could be explained because yellow coloration on plumage is a result of reflection of light by structural tissue and carotenoid light absorption (Shawkey and Hill 2005). The yellow-olive coloration of Wilson's Warbler tail feathers is the result of an structural/melanic coloration (Gray 1996) combined to a carotenoid coloration more than a pure carotenoid coloration as expected in pure yellow coloration. Carotenoid coloration depends on the ingested food which makes it a good indicator of body condition (Hill 1999); however, it is different for structural and melanic coloration. Structural color has been suggested to be more sensitive to stress than to body condition (Peters et al. 2011) and it depends more on genetics (Shawkey et al. 2006) as is also the case of melanic color (Bize et al. 2006, Roulin and Ducrest 2013) that is endogenously produced by birds.

We also did not find a relationship between winter body condition index and any of the territory characteristics we measured. This could be attributed to the high plasticity of generalist species such as Wilson's Warbler and to the fact that we compared territories within the same habitat, the cloud forest, that has been suggested to be high quality habitat for the species (Ruiz-Sánchez et al. in revision). Plasticity of habitat affinity allows certain resilience to habitat disturbance. Cerulean Warbler has shown to be able to adapt to habitat modification by modifying territory size among other behavioral strategies (Jones et al. 2001). Thus, it is possible that Wilson's Warbler is compensating habitat differences and its related resource limitations by adjusting behavior to accordingly set a territory size (Smith and Shugart 1987, Jones et al. 2001).

Rapid tropical habitat modification and destruction makes it crucial to properly select the habitats to be subject of preservation efforts. Our study shows how even for species able to inhabit a diverse range of habitats during the winter, there are specific habitat characteristics that significantly influence birds wintering opportunities and possibly future survival and reproductive success. In our study both shrub and tree abundance relationship to summer body condition (feather microstructure), territory size and food abundance indicates that this two winter habitat traits are favorable for Wilson's Warbler and could also be favorable to other migratory birds with similar needs.

There are carry-over effects from summer to winter that highlight the importance of conserved forests, with high shrub and tree abundance, as high-quality habitats for migratory birds in both breeding and wintering grounds. To our knowledge this is the first study to evaluate carry-over effects of summer body condition on winter opportunities for migrating birds, which may have uncertain population effects that still need to be addressed by further research. In particular, the dual effects of summer body condition on winter opportunities, and winter body condition on summer breeding performance, may have accumulative long-term effects on populations of migratory birds that are largely unknown and little understood.

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FIGURE LEGENDS

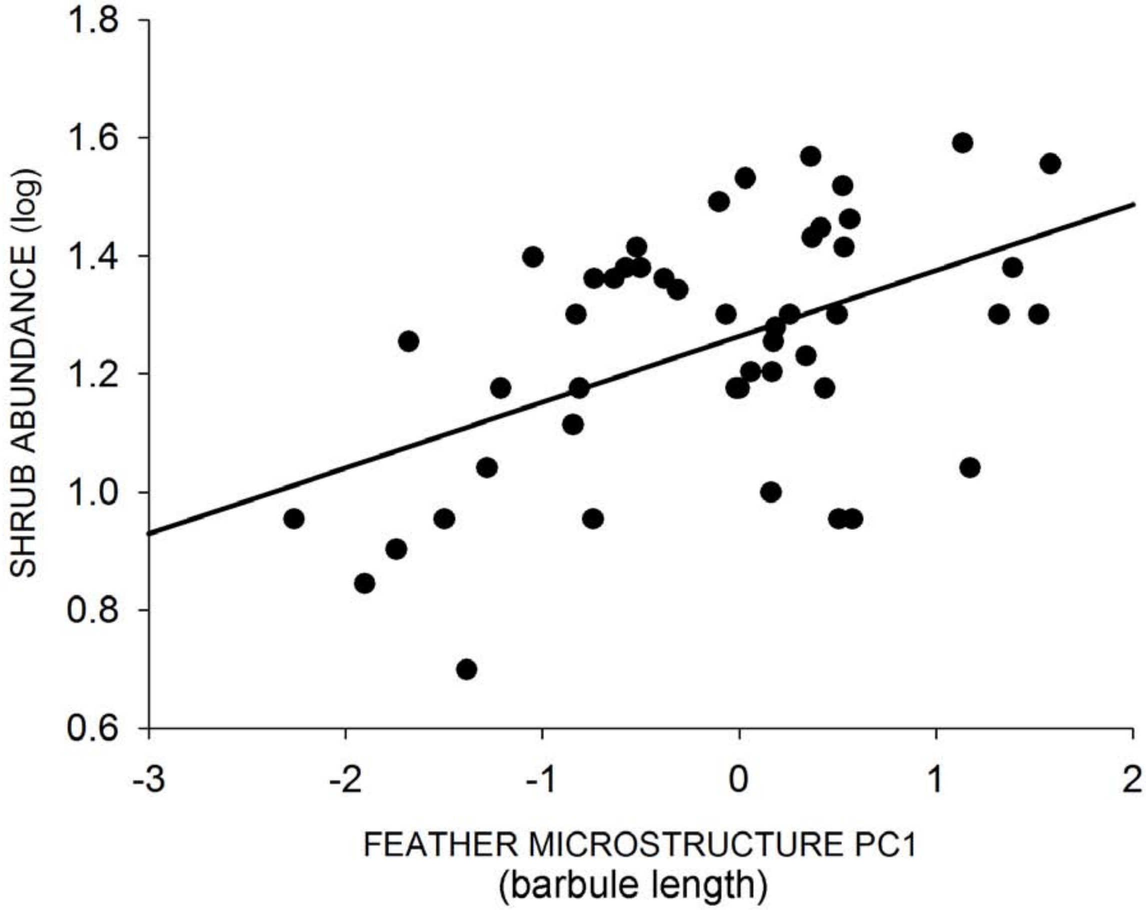
Figure 1. Linear regression of shrub abundance in winter territories of Wilson's Warblers related to Principal Component 1 (feather micro structure) of Wilson's Warbler's summer body condition. Low negative values for PC1 represent birds with higher summer body condition.

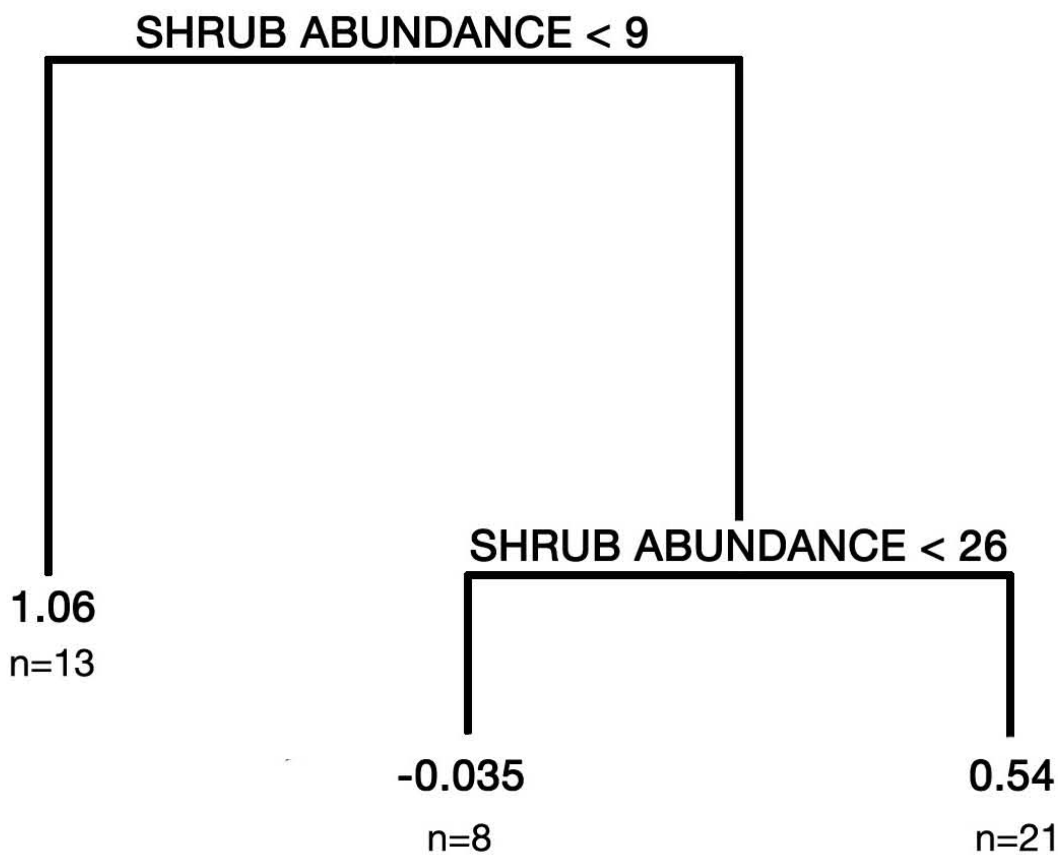
Figure 2. Regression tree for summer body condition (PC1: feather microstructure) predicted by shrub abundance in winter territories. Split values represent threshold levels for the predictor variable, with mean trait values and sample size indicated at each terminal node. Lower values of PC1 indicate better summer body condition.

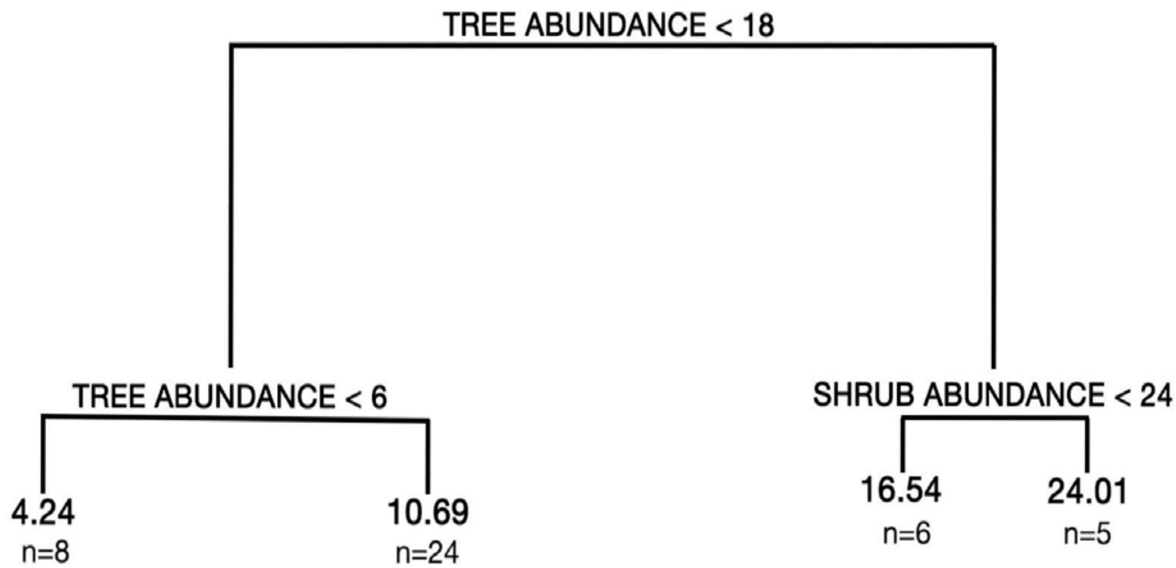
Figure 3. Regression tree for arthropod food abundance index predicted by shrub and tree abundance in winter territories of Wilson's Warblers. Split values represent threshold levels for the predictor variable, with mean trait values and sample size indicated at each terminal node.

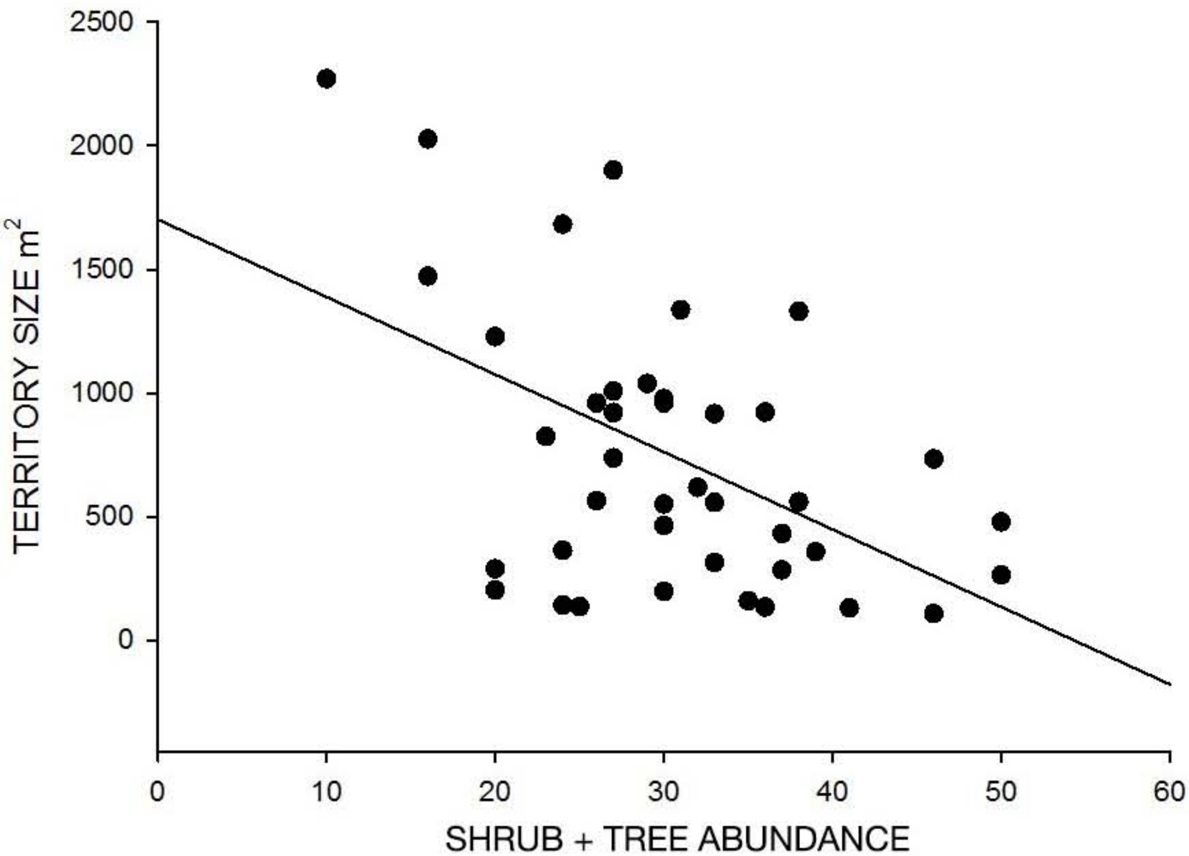
Figure 4. Linear regression of winter territory size related to density of woody vegetation (shrub and tree abundance) for Wilson's Warblers in cloud forest of Veracruz, Mexico.

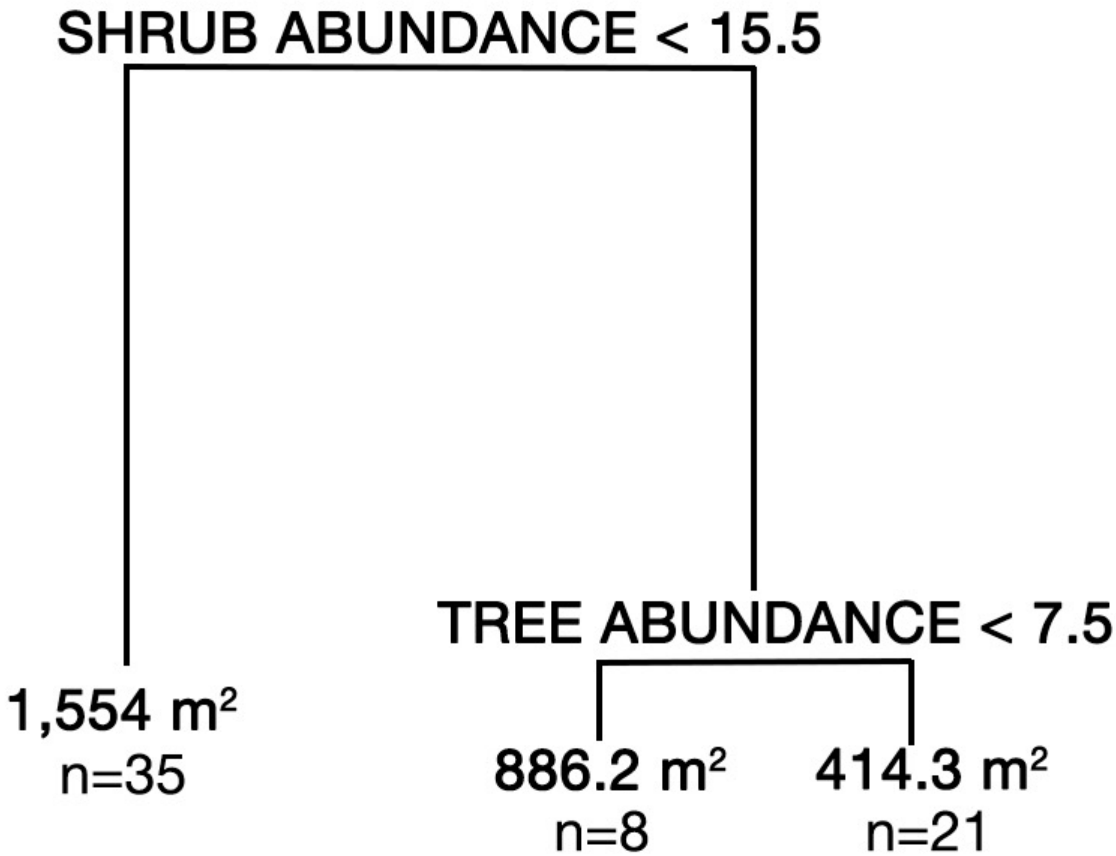
Figure 5. Regression tree for Wilson's Warbler winter territory size predicted by shrub and tree abundance in cloud forest of Veracruz, Mexico. Split values represent threshold levels for the predictor variable, with mean trait values and sample size indicated at each terminal node


SHRUB ABUNDANCE (log)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
-3
-2
-1
0
1
2
FEATHER MICROSTRUCTURE PC1
(barbule length)


SHRUB ABUNDANCE < 9
SHRUB ABUNDANCE < 26
1.06
n=13
-0.035
n=8
0.54
n=21


TREE ABUNDANCE < 18
TREE ABUNDANCE < 6
SHRUB ABUNDANCE < 24
4.24
n=8
10.69
n=24
16.54
n=6
24.01
n=5


2500
2000
1500
1000
500
0
TERRITORY SIZE m^2
0
10
20
30
40
50
60
SHRUB + TREE ABUNDANCE


SHRUB ABUNDANCE < 15.5
TREE ABUNDANCE < 7.5
1,554 m²
n=35
886.2 m²
n=8
414.3 m²
n=21

DISCUSIÓN GENERAL

El presente estudio permitió ampliar el conocimiento acerca de la ecología de *Cardellina pusilla* y proporcionó información relevante y necesaria que puede ser utilizada para re-evaluar y mejorar las estrategias de conservación para la especie. Asimismo y quizá aún más importante es el potencial uso de este conocimiento para entender procesos ecológicos de otras especies de aves migratorias cuyas poblaciones se encuentran también disminuyendo y requieren de estrategias más expeditas.

En primer lugar el modelado de nicho ecológico y la evaluación de las distancias ecológicas permitieron evaluar la ecología de la especie de estudio a un nivel continental. En particular, se determinó que los dos grupos genéticos y geográficos de *C. pusilla*, que han sido sugeridos como especies crípticas (Irwin et al. 2011), son también ecológicamente distintos. El presente estudio mostró que existen amplias diferencias climáticas entre los grupos del este y del oeste a lo largo de todo su rango de distribución, tanto en la época de reproducción en el verano, como durante el invierno. Se encontró que el grupo del Este es climáticamente más restringido. Basado en las predicciones de los modelos de nicho, ambos grupos pueden potencialmente ocupar ∽50% de la distribución del grupo del este. Sin embargo, la distribución registrada de los grupos del este y el oeste es parapátrica en verano y coincide solo en pequeñas áreas de su distribución de invierno; a tal grado que estudios previos no pudieron recabar suficientes datos acerca de la distribución invernal del grupo del este (Kimura et al. 2002, Irwin et al. 2011).

Esto lleva a concluir que existen otros factores no climáticos y probablemente bióticos involucrados en la delimitación de la distribución geográfica de estos grupos dentro del complejo *C. pusilla*. A la fecha no existen coberturas en las que se incluyan interacciones biológicas que pudieran mejorar las predicciones de los modelos de nicho para la especie. Es posible que la distribución parapátrica de los grupos del este y el oeste sea un indicador de que los grupos estén evitando coexistir en el mismo territorio de otra especie cuyo rol ecológico es similar y significaría una fuerte competencia por recursos y un alto gasto energético (Bourski y Forstmeier 2000).

Los resultados de los tres métodos empleados para evaluar la similitud de los nichos ecológicos de los dos grupos de *C. pusilla* nos permitieron apoyar la hipótesis de que la especie es en realidad un complejo que alberga dos especies crípticas (Irwin et al. 2011). A su vez permite sugerir que se debería de evaluar el estatus de vulnerabilidad de *C. pusilla* separando estos dos grupos y tomando en cuenta las diferencias tanto morfológicas como genéticas y ecológicas. Es posible que bajo este criterio el estatus de vulnerabilidad sea distinto entre grupos y distinto al que reciben actualmente al evaluarse en conjunto, dado que probablemente se ubicarían en categorías más específicas de uso de hábitat, mientras actualmente es considerada una especie generalista de amplia distribución (Hutto 1981, Rojas-Soto et al. 2010, Berlanga et al. 2010).

El segundo enfoque de evaluación del presente estudio es a nivel local basado en distintos grados de perturbación del bosque mesófilo. Esto permitió mostrar que el grado de perturbación del hábitat influye sobre la densidad de la especie y el tamaño de los territorios que estable durante el invierno. Aun cuando estudios acerca del uso de hábitat durante la época reproductiva en Norteamérica indiquen que *C. pusilla* puede hacer uso de hábitats perturbados y no perturbados de manera similar (Hejl et al. 1995; Desrochers et al. 2012), nuestra evaluación del efecto de la perturbación del hábitat sobre su ecología invernal indica que el bosque conservado brinde mejores oportunidades para la especie que el bosque bajo perturbación, sea esta perturbación media o alta.

La conclusión de que el bosque mesófilo conservado representa un hábitat de alta calidad para *C. pusilla* se extrae dado que la densidad de la especie es mayor en sitios conservados. La densidad de aves puede ser indicador de calidad de hábitat, donde altas densidades corresponde a hábitats más adecuados con suficientes recurso para mantener a la población (Gilroy and Sutherland 2007). Asimismo, el tamaño de territorio fue menor en el bosque conservado, sugiriendo que en este hábitat recursos tales como el alimento sean abundantes, dado que tamaños de territorio menores han sido relacionados a altas abundancia de alimento mientras que tamaños de territorio mayores han sido relacionados a baja abundancia de alimento (Verner 1977, Myers et al. 1979). Esto coincide con lo encontrado en otros estudios donde se muestra que la abundancia de artrópodos, que es el principal recurso alimenticio de *C. pusilla*, es mayor en hábitats con alta humedad y alta precipitación, como las que se encuentren en los bosques (Latta y Faaborg 2002, Studds y Marra 2005, 2007, Brown y Sherry 2006, Smith et al. 2010).

Encontré que la condición física invernal y el tamaño del territorio de *C. pusilla* mostró poca variación entre años en el bosque conservado, indicando que esto representa un hábitat más adecuado para la especie, diferente a lo que sucede en los bosques perturbados donde se registró alta variación de la condición física entre años. Tal variación en los bosques perturbados indica que se trata de un hábitat inestable que podrían funcionar como una trampa ecológica (Ekroos et al. 2012) dependiendo de las condiciones que presente el hábitat en cada temporada.

Las diferencias encontradas cobran mayor importancia al tratarse de la evaluación de características ecológicas dentro de un mismo hábitat. Estudios anteriores han encontrado diferencias en la ecología invernal de las aves entre hábitats distintos, con condiciones más contrastantes (Marra et al. 1998, Latta y Faaborg 2002, Sherry y Holmes 1996, Saino et al.

2004). Haber encontrado diferencias bajo distintas condiciones del mismo hábitat de bosque mesófilo indica que la especie es altamente sensible a cambios en la estructura de la vegetación.

A nivel individual para *C. pusilla*, se mostró que la condición física de verano influye sobre la selección de territorios de invierno. Los individuos que expresaron alta condición física de verano seleccionaron áreas con alta abundancia de arbustos para establecer sus territorios invernales. Aunado a esto, encontré que abundancia de arbustos fue el principal factor que influye en el tamaño de territorio y en la abundancia de alimento; donde a mayor abundancia de arbustos hay mayor abundancia de alimento y los territorios son de menor tamaño. Esta relación indica que los individuos con baja condición física de verano estarán en desventaja para elegir territorios al inicio del invierno y probablemente estarán también en desventaja para regresar a los territorios de reproducción, con las consecuencias, que esto pueda significar, en el éxito reproductivo (Marra et al. 1998).

El presente estudio aporta información novedosa y relevante. Es el primer estudio en mostrar el efecto que tiene la condición física de verano sobre las oportunidades que las aves tendrán durante el invierno. Asimismo, este estudio muestra de manera clara la influencia que tiene la perturbación humana del hábitat sobre aspectos clave de la ecología invernal de las aves migratorias. Tal como lo muestra nuestro estudio, la modificación del hábitat tiene efectos inmediatos y efectos en estaciones subsecuentes que se desconoce si pudieran a llegar a ser acumulables, si las estrategias de compensación fisiológicas y conductuales no fueran suficientes ante las condiciones constantemente cambiantes del hábitat. La pérdida de hábitat invernal en México se debe en mayor medida a la alta tasa de deforestación, que es una de las más altas de Latinoamérica (Askins et al. 1990). Particularmente en el Centro del Estado de Veracruz la principal amenaza es el crecimiento urbano no planeado y la transformación de uso de suelo mal dirigida que ha llevado a la perdida de la mayor parte de la cobertura original d los bosques en la región (Williams-Linera 2012). Dada la acelerada tasa de detrimento del hábitat invernal natural se esperaría que el efecto negativo en las poblaciones de aves sea evidente en el futuro cercano, ya que cambios los cambios, aparentemente no drásticos, dentro de un mismo tipo de hábitat muestran repercusiones en una especie generalista de la cual se espera amplia plasticidad.

Los esfuerzos de conservación pueden ser mejor dirigidos cuando se tiene conocimiento de los efectos del hábitat sobre el comportamiento y características poblaciones de las aves migratorias. El conocimiento de dichos efectos en los territorios de invierno es específicamente importante dado que el hábitat invernal tiene importantes efectos sobre el éxito reproductivo de las aves (Marra et al. 1998, Norris et al. 2004; Reudink et al. 2009). Tras analizar los resultados de los estudios aquí incluidos hago énfasis en la importancia de conservar activamente los remanentes del bosque mesófilo de montaña, cuya extensión ha sido gravemente reducida (Williams-Linera et al. 2013), así como los acahuales de bosque mesófilo que puedan ser restaurados, dado que la densidad, el tamaño de territorio, la condición física tanto de verano como de invierno indican que este es un hábitat de alta calidad para la especie y posiblemente para otras aves migratorias neotropicales. He podido mostrar que aun cuando los individuos son capaces de compensar las limitaciones de recursos mediante su plasticidad fisiológica y de comportamiento (Weber y Hedenström 2001, Pierce y McWilliams 2005), la perturbación del hábitat influencia de manera negativa a las aves y los hábitats perturbados ofrecen condiciones subóptimas para las aves migratorias. Dicha relación resulta aún más preocupante dado que se desconoce el costo inmediato y en futuras temporada que pueda tener la compensación por diferencias en la disponibilidad de recursos. El conocimiento acerca de cómo utilizan las aves sus hábitats invernales y de verano hará posible proponer estrategias más apropiadas para su conservación.

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