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Efectos del cambio climático sobre las poblaciones de lepidópteros de la Sierra de Guadarrama. Modelos predictivos.

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CERTIFICAN:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: "**Efectos del cambio climático sobre las poblaciones de lepidópteros de la Sierra de Guadarrama. Modelos Predictivos**", son aptos para ser presentados por el Ldo. Javier Gutiérrez Illán ante el Tribunal que en su día se consigne, para aspirar al Grado de Doctor en Ciencias Ambientales por la Universidad Rey Juan Carlos de Madrid.

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INTRODUCCIÓN

Antecedentes

El cambio climático global y la pérdida de hábitat constituyen hoy en día las principales amenazas a la biodiversidad (Wuethrich, 2000; Walther, et al., 2002; Parmesan & Yohe, 2003; Root el at., 2003; Parmesan, 2006). El cambio climático no solo se traduce en un aumento de las temperaturas, que han experimentado incrementos de hasta 0.6ºC en los últimos 100 años (Houghton, 1996; Gian-Reto et al., 2003), en su mayoría en la segunda mitad del siglo XX (IPCC, 2007), sino también en la disminución de las grandes masas de hielo terrestres, el aumento del nivel del mar, y una mayor frecuencia de eventos climáticos extremos, como huracanes y grandes inundaciones, entre otros. Éstos procesos podrían incluso agravarse según las previsiones más pesimistas del IPCC. No obstante, los cambios regionales, que son espacialmente heterogéneos, son mucho mas representativos a la hora de evaluar las respuestas de los organismos, las poblaciones y las comunidades ecológicas al cambio climático (Hughes, 2000; Gian-Reto et al., 2003).

Las repercusiones del calentamiento climático sobre los sistemas biológicos pueden ser muy diversas e incluso pueden interaccionar con otros motores de cambio como la fragmentación y las modificaciones en los usos de suelo (Thuiller et al., 2004). Sin embargo, los cambios sobre los que existe una mayor evidencia son los referentes a los desplazamientos en distribución y las alteraciones fenológicas de las especies (Wilson et al., 2007a).

Desplazamientos en distribución de las especies

Evidencias de cambios recientes en distribución

Existen ya numerosos estudios que han documentado cambios en la distribución (Huntley et al, 1995; Thomas et al., 2004; Guisan & Thuiller, 2005; Araújo & Luoto, 2007) y riqueza

(Stefanescu et al., 2004; White & Kerr, 2006; Marmion et al., 2009) de las especies asociados con el calentamiento climático, e incluso en algunos casos, procesos de extinción directamente relacionados con este calentamiento (Easterling, 2000). Concretamente, se han observado desplazamientos de la distribución geográfica de numerosas especies hacia latitudes y altitudes más altas (Parmesan et al., 1999; Parmesan & Yohe, 2003; Hickling et al., 2006, Wilson et al., 2007a), de manera que en las comunidades ecológicas se ha incrementado la dominancia de especies adaptadas a condiciones climáticas más cálidas (Chapin et al., 1995; Holbrook et al., 1997; Sagarin et al., 1999; Beaugrand et al., 2002), y la riqueza de especies ha aumentadoo en las latitudes templadas más elevadas (Menéndez et al., 2006). Sin embargo, debido a que la pérdida y degradación del hábitat interaccionan con los efectos del cambio climático, los incrementos en la diversidad de especies a escala geográfica se han producido más lentamente de lo que cabría esperar únicamente como resultado de la variación en el clima. De esta forma, las especies generalistas y con mayor capacidad de dispersión han visto aumentada su contribución relativa en las comunidades ecológicas a expensas de las especies especialistas y más sedentarias, cuya distribución se han visto afectada en mayor medida por la pérdida y fragmentación de su hábitat (Warren et al., 2001; Julliard et al., 2003; Menéndez et al., 2006).

Se espera que las especies que viven en las regiones montañosas puedan responder de forma más rápida al cambio climático, debido a que frecuentemente dichas regiones albergan hábitats con un menor estado de alteración y a que los acusados gradientes altitudinales facilitan los desplazamientos hacia zonas con climas más adecuados en distancias relativamente cortas. Numerosas especies han cambiado ya sus distribuciones a consecuencia del calentamiento climático, observándose extinciones en las zonas bajas y colonizaciones locales en las regiones más elevadas (Pounds et al., 1999; Hill et al., 2002; Peñuelas & Boada, 2003; Franco et al., 2006). Sin embargo, cabe también la posibilidad de que las regiones de montaña puedan sufrir de forma acentuada e irreversible los efectos del cambio climático (Fielding et al., 1999), debido a que las especies que allí habitan tienen un limitado espacio para desplazarse altitudinalmente en busca de temperaturas menos extremas (Wilson et al., 2005) y a que las colonizaciones locales por parte de especies de zonas mas bajas probablemente no lleguen a compensar las pérdidas de especies de las zonas progresivamente mas altas (Wilson et al., 2007b). Esto se debe a que en muchas ocasiones, el deplazamiento migratorio altitudinal no es posible porque las áreas mas altas ya han sido colonizadas o no hay más territorio al que desplazarse (Körner, 2007). El área habitable de estas especies, por tanto, puede verse reducida, especialmente en las regiones más montañosas de Europa como la Península Ibérica. Sin embargo, a pesar de que haya un número cada vez mayor de evidencias que revelan cambios en distribución asociados con el calentamiento climático, existe un importante desequilibrio a favor de aquellas que apuntan a expansiones en los límites de distribución fríos con respecto a las que muestran retracciones en los cálidos (Thomas et al., 2006). Uno de los principales objetivos de esta tesis es precisamente evaluar los cambios en distribución altitudinal de las mariposas de una zona de montaña que ha sufrido cambio climático reciente, la Sierra de Guadarrama, donde se espera que haya una importante retracción de los límites de distribución inferiores.

Modelos predictivos de distribución y riqueza de especies

Las distintas situaciones contempladas por los modelos climáticos globales apuntan a incrementos de temperatura para las próximas décadas en general mayores que los sufridos durante el siglo XX (IPCC, 2007). Ello supone un importante reto a la hora de evaluar cuáles son las posibles consecuencias de estos cambios futuros sobre la biodiversidad. En ese sentido, existe una disciplina dentro de la ecología, la modelización predictiva de la distribución y riqueza de especies, que está cobrando una importancia cada vez mayor. Estos modelos son ecuaciones matemáticas mediante las cuales es posible predecir la probabilidad de ocupación o la abundancia de una especie, o la riqueza de especies de una comunidad en base a variables ambientales relacionadas, por ejemplo, con el clima y los usos del suelo

(Guisan & Zimmermann, 2000; Johnson & Omland, 2004). Aunque las bases ecológicas sobre las que se asientan estos modelos son ya parte de la ecología clásica, el desarrollo de nuevas técnicas estadísticas y de los Sistemas de Información Geográfica (SIG) ha supuesto que los modelos de distribución y riqueza sean una de las disciplinas más activas de la ecología actual. A pesar de tratarse en su mayoría de técnicas estáticas y probabilísticas, ya que tratan de relacionar las distribuciones geográficas actuales de las especies con el ambiente, la variedad de procedimientos utilizados está en continuo desarrollo. En muchos casos, las especies utilizadas no han sido suficientemente estudiadas como para conocer sus respuestas a un cambio en el ambiente (Woodward & Cramer, 1996; Guisan & Zimermann, 2000). Por estas razones, la modelización geográfica de procesos ecológicos como los cambios en la distribución (Pearson & Dawson, 2003; Bradley & Fleishman, 2008; Araújo & Luoto, 2007) y riqueza de las especies (White & Kerr, 2007; Nogués-Bravo et al., 2008) ha experimentado recientemente un notable desarrollo, en los que el cambio climático y la destrucción de hábitat se han erigido como los principales causantes de estos cambios.

Recientemente se ha abierto un debate en cuanto a la importancia relativa de los tipos de variables empleadas en la modelización de la distribución y riqueza de especies (Thuiller et al., 2004; Pearson et al., 2004; Gutiérrez Illán et al., en prensa). Está comúnmente aceptado que, trabajando a grandes escalas espaciales, la distribución y riqueza de especies está determinada en su mayor parte por factores topoclimáticos, mientras que la importancia del hábitat y uso del suelo aumenta cuando nos desplazamos a escalas regionales o locales (Rahbek & Graves 2001; Thuiller et al, 2004; Luoto et al., 2007). Sin embargo, en regiones de montaña, donde las condiciones climáticas varían enormemente en pequeñas distancias debido al gradiente altitudinal, la efectividad de los modelos topoclimáticos frente a los de hábitat está aún por evaluar. Buena parte de esta tesis intenta dar respuesta a esa inquietud, aplicando diversas técnicas de modelización a distintas series de datos de campo tomados a escala regional, utilizando como sistema de estudio las mariposas de la Sierra de Guadarrama.

Cambios en los patrones fenológicos de las especies

Además de los cambios en espaciales en distribución, el cambio climático ha provocado cambios temporales en los ciclos de vida de las especies. Durante los últimos años, el estudio de los cambios en la fenología de las especies se han convertido en una de las principales herramientas para la detección y evaluación de los efectos del cambio climático sobre la biodiversidad (Peñuelas & Filella, 2001; Walther et al., 2002; Peñuelas et al., 2002). La mayoría de los estudios ponen de manifiesto efectos sobre diversos procesos fisiológicos y ecológicos de las especies (Parmesan & Yohe, 2003; Root et al., 2003), como el adelanto en la primera aparición y la fecha media de vuelo de los insectos adultos asociado con el aumento de temperatura (Roy & Sparks, 2000; Forister & Shapiro, 2003). Estos efectos, reflejados en una dimensión temporal, tienen también su contrapartida en una dimensión espacial, como los gradientes latitudinales y altitudinales (Wilson et al., 2007a). Por ejemplo, la emergencia y los períodos de vuelo de los insectos pueden verse retrasados en latitudes y altitudes superiores debido a que las temperaturas son más bajas en esas zonas (Gutiérrez & Menéndez, 1998; Bird & Hodkinson, 1999; Fielding et al., 1999; Roy & Asher, 2003). Sin embargo, en el caso de algunos insectos, estos retrasos fenológicos inducidos por el clima pueden ser atenuados mediante adaptaciones locales relacionadas con la selección de distintos microhábitats en diferentes partes del gradiente o con modificaciones en los ciclos de vida (Thomas, 1993).

Para el estudio de los cambios fenológicos potenciales asociados con el calentamiento global, son necesarias series temporales de datos que recojan los aspectos más importantes en el ciclo de vida de las poblaciones en estudio. Este tipo de bases de datos son relativamente frecuentes en algunos países del norte de Europa (como por ejemplo el Buttefly Monitoring Scheme del Reino Unido y los similares de Países Bajos y National Butterfly Recording Scheme de Finlandia (Saarinen et al., 2002)), pero mucho más escasos en latitudes más bajas (pero véase el caso del nordeste de España con el Catalan Butterfly Monitoring Scheme, CBMS, Stefanescu et al., 2000). Por otra parte, en estas bases de datos existe normalmente una gran deficiencia de registros en áreas de montaña, de manera que la información sobre la variación geográfica de los cambios fenológicos es muy limitada (aunque el CBMS está incluyendo ya localidades de los Pirineos). Esta tesis pretende cubrir esas deficiencias mediante el análisis de los cambios fenológicos a lo largo de un gradiente altitudinal de la Sierra de Guadarrama utilizando las mariposas como organismos de estudio.

Objetivos generales y estructura de la tesis doctoral

El principal objetivo de esta tesis es examinar los cambios potenciales de distribución, diversidad y fenología de especies en relación con el cambio climático reciente en una región donde un elevado número de especies presentan sus límites meridionales o “cálidos” de distribución. Para ello, se eligió como sistema de estudio las mariposas de la Sierra de Guadarrama, debido a la sensibilidad de éstos organismos a los cambios ambientales y a las características biogeográficas de esta región (para más detalles, véase el apartado de Metodología general). Así mismo, dentro de esta tesis se pretenden diseñar herramientas que sean útiles para la predicción de los posibles cambios futuros sobre las especies de mariposas de la región como consecuencia de las distintas situaciones de cambio climático proyectadas por los Modelos de Circulación General (MCG) desarrollados hasta la fecha (IPCC, 2007).

Los objetivos concretos son los siguientes:

1.- Determinar si la distribución geográfica y/o altitudinal de las mariposas de la Sierra de Guadarrama han cambiado entre 1967-73 y la actualidad, y si los cambios detectados son consistentes con las variaciones climáticas manifestadas durante ése mismo periodo.

2.- Examinar si es posible predecir la distribución, riqueza y composición de las especies de de mariposas de la Sierra de Guadarrama mediante modelos basados en información topoclimática y de cobertura del terreno procedentes de distintas localidades situadas a lo largo de un gradiente altitudinal.

3.- Estudiar los patrones fenológicos de las poblaciones de mariposas de la Sierra de Guadarrama a lo largo de un gradiente altitudinal durante un periodo de cinco años (2004-2008) y determinar las fuentes de variación de dichos patrones.

Para cumplir los objetivos propuestos, la presente tesis incluye cuatro capítulos:

-El **primer capitulo** está dedicado al estudio de los cambios en la distribución de las especies durante un período de calentamiento climático reciente, y evalúa los ascensos de los límites altitudinales y sus consecuencias en cuanto a la reducción del área climáticamente habitable. Los resultados que corresponden a la comparación entre el periodo 1967-73 y el año 2004 han sido publicados en la revista *Ecology Letters*, y en este capítulo además, se complementan dichos análisis con los datos obtenidos de los muestreos de campo de 2005.

-El **segundo capítulo** comprende la elaboración y evaluación de modelos de distribución y abundancia de las especies a partir de información ambiental, determinando la importancia relativa de los factores topoclimáticos y de cobertura del terreno en cuanto a su capacidad predictiva. El presente capítulo se encuentra aceptado y en prensa en la revista *Global Ecology and Biogeography*.

-El **tercer capítulo** se basa en la elaboración de modelos de riqueza y composición de especies, evaluándose también la importancia relativa de los factores topoclimáticos y de uso de suelo en cuanto a su capacidad predictiva. Este capítulo se encuentra actualmente en proceso de revisión en la revista *Journal of Biogeography*.

-Por último, el **cuarto capítulo** examina los patrones fenológicos de las poblaciones de mariposas en un gradiente altitudinal, atendiendo al retardo en la fecha de aparición a lo largo del gradiente y a los determinantes de la variación interspecífica en dicho retardo.

Los resultados obtenidos son de especial interés en el ámbito de la investigación básica, pero también en el de la biología de conservación, ya que las conclusiones que se deriven servirán para tomar decisiones de protección de las especies más vulnerables al cambio ambiental con una base infinitamente más sólida que la existente en la actualidad.

Metodología general

Área de estudio: La Sierra de Guadarrama

La Península Ibérica es una de las regiones con mayor biodiversidad de insectos de Europa (van Swaay & Warren, 1999) y en sus sistemas montañosos se concentra la mayor parte de ésta diversidad. Su fauna de mariposas es especialmente rica, albergando 220 de las 576 especies presentes en toda Europa (van Swaay & Warren, 1999; Stefanescu et al., 2004). Sin embargo, la mayoría de los estudios que utilizan las poblaciones de lepidópteros como indicadores del cambio climático en Europa se han llevado a cabo en el Reino Unido, que es una zona insular con una fauna relativamente pobre (por ejemplo, Thomas et al, 2001; Warren et al., 2001). En particular, la Sierra de Guadarrama representa un "hotspot" en cuanto a diversidad lepidopterológica (Van Swaay & Warren, 2003; García-Barros et al., 2004), lo que pone de manifiesto la necesidad de estudiar y conocer los factores que definen y generan dicha diversidad. Por otra parte, desde el último tercio del siglo XX (1967-73), la temperatura media en la sierra de Guadarrama ha subido alrededor de 1.3°C (Wilson et al., 2005), de manera que las poblaciones de lepidópteros diurnos de la región, que en muchos casos encuentran aquí su limite latitudinal inferior de distribución, podrían verse alteradas siginificativamente. Por estos motivos, este sistema montañoso constituye un excelente sistema para el estudio de los efectos del cambio climático sobre las las poblaciones de lepidópteros en las últimas décadas.

La Sierra de Guadarrama (Sistema Central) es el límite montañoso situado al norte de la Comunidad de Madrid que se extiende en un eje de Sudoeste a Noreste. Es la cadena montañosa por muchos denominada como la "Sierra de Madrid", un espacio natural singular, de gran belleza y alta diversidad biológica. El punto más alto de éste sistema montañoso se encuentra en el pico Peñalara, con sus 2430 metros sobre el nivel del mar (Figura 1).

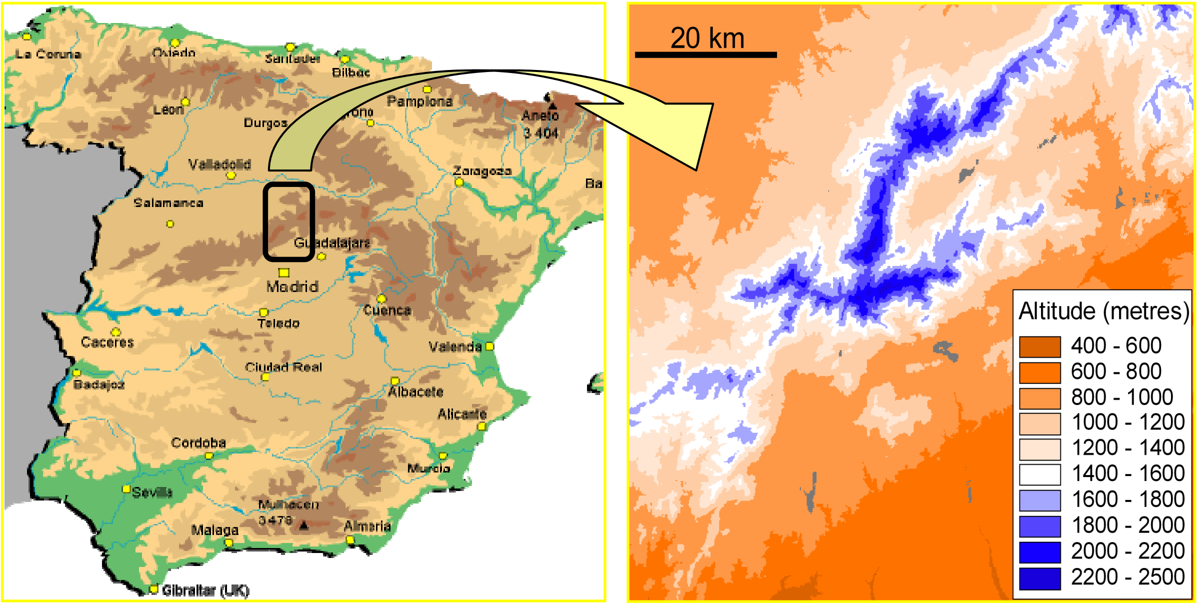

Figura 1 Contexto geográfico de la Sierra de Guadarrama y mapa digital del terreno (MDT) de la zona de estudio, mostrando la altitud estratificada en bandas de 200 metros.

El sistema de estudio abarca 10800 kilómetros cuadrados, localizados en una cuadrícula de 90 x 120 km situada en el centro de la Península Ibérica, incluyendo la Sierra de Guadarrama y sus alrededores. Se extiende desde la esquina suroeste en 40º20'N 4º40'W (referencia UTM 30TUK8050) hasta la noreste en 41º28'N 3º36'W (UTM 30TVL7070) (Figura 1). El área está bordeada por planicies con altitudes comprendidas entre los 500 (hacia el sur) y los 700 m (hacia el norte).

Los principales tipos de vegetación dominante en la zona son los bosques perennifolios (mayoritariamente *Quercus rotundifolia*) en altitudes comprendidas hasta los 1000 m, los bosques caducifolios (mayoritariamente *Quercus pyrenaica*) en altitudes entre los 1000 y 1500 m, y los bosques de coníferas (mayoritariamente *Pinus sylvestris*) en altitudes aproximadamente entre 1500 y 2000 m. Los matorrales y pastos abiertos están presentes en todas las altitudes, incluyendo la zona de cumbres situada por encima de los 2000 m (Rivas-Martínez *et al.*, 1987) (Figura 2).

Figura 2 Punto inicial del transecto de "La Pedriza" (1050 m.). Zona de muestreo con pastos abiertos y matorrales, en el sector sur de la Sierra de Guadarrama. (Fotografía: Javier Gutiérrez Illán)

El clima del área de estudio se puede clasificar como mediterráneo continentalizado, caracterizado por un rango de variación térmica muy marcado entre el invierno y el verano y por presentar un periodo estival extremadamente seco. El marcado gradiente altitudinal de la zona supone además un fuente adicional de variación climática, con temperaturas por debajo de los -15ºC en las cotas superiores y de más de 35ºC en las zonas más bajas. Algo similar ocurre con las precipitaciones anuales, pudiendo oscilar entre los 700 y los 2500 mm.

La información obtenida procede de una serie de localidades con diferentes condiciones climáticas, altitud, estructura de las poblaciones y uso del hábitat por parte de los insectos, con el fin de contemplar y modelizar las repuestas de las especies a los cambios en las condiciones ambientales. Para abordar los objetivos de esta tesis se utilizaron, por un lado, los datos obtenidos en el campo mediante muestreos de mariposas en transectos lineales y por otro, datos que recogen la variabilidad ambiental de la zona de muestreo. Los datos de campo se dividen en dos grupos principales. El primero de ellos, utilizado en el primer capítulo, fue recogido durante los años 1967-73 por el profesor Victor J. Monserrat en la Sierra de Guadarrama y alrededores (Monserrat, 1976). Se trata de una serie temporal (ocho años) de datos de abundancia recogidos en campo durante la época de vuelo de las mariposas. Dichos datos son de un valor excepcional, ya que la información observacional de diversidad lepidopterológica de esta antigüedad es extremadamente rara en la Peninsula Ibérica, aunque es preciso resaltar que el esfuerzo de muestreo estuvo controlado de manera menos estricta que en los muestreos actuales. El segundo grupo de datos de campo fue recogido por el grupo de investigación en la misma zona de muestreo, durante los años 2004 a 2008. Estos 5 años de datos se han tratado de manera independiente y han sido utilizados en todos los capítulos de la presente tesis. La variabilidad ambiental del sistema de estudio se recogió a partir de datos climáticos procedentes de estaciones meteorológicas de la zona, modelos digitales del terreno y capas de coberturas del terreno vectoriales generadas a partir de distintas fuentes (fotografía aérea y de satélite, fundamentalmente), de las cuales se obtuvo la información de cobertura del terreno, hidrología y geología necesarias para la caracterización de las localidades de muestreo.

Las localidades de muestreo son zonas abiertas de hábitat natural o semi-natural y fueron elegidas siguiendo una estratificación altitudinal. Los principales hábitats representados en los transectos fueron matorrales mediterráneos (Figura 3a), claros de robledales (Figura 3b) y pinares (Figura 3c), y praderas de alta montaña (Figura 3d). Las poblaciones de mariposas del área de muestreo se registraron mediante la realización de conteos siguiendo transectos lineales estandarizados de 500 metros (Pollard & Yates, 1993), incluyendo todos aquellos individuos dentro de un área de 5 x 5 metros cuadrados (5 m hacia delante y 2.5 m a ambos lados del investigador). Estos conteos se realizaron durante la época de vuelo de los lepidópteros cada dos (transectos para el estudio de la fenología) o tres semanas (resto de localidades), desde el mes de abril a octubre en los años 2004-2006, y desde marzo a octubre en 2007-2008 (Tabla 1).

Tabla 1 Distribución de los periodos de muestreo en función de los capítulos en los que se han utilizado los datos de campo y resultados obtenidos. También se indican el numero de localidades visitadas y el objetivo principal.

	Período (años de muestreo)	**Nº de localidades**	**Objetivo**
Capítulo I	1967-73 / 2004-2005	66 / 180	Cambios temporales en distribución
Capítulo II	2004, 2005	180	Modelos de distribución y abundancia
Capítulo III	2004, 2005	180	Modelos de riqueza y composición
Capítulo IV	2004, 2005, 2006, 2007, 2008	20 (2004-2005), 34(2006) 40 (2007-2008)	Efectos del gradiente altitudinal en fenología

Figura 3. Aspecto de algunas localidades muestreadas en la Sierrra de Guadarrama. a) Transecto de "*La Pedriza*", dominado por pastos y matorrales; b) Transecto de "*El Palancar*", dominado por claros en robledales mediterráneos; c) Transecto de "*Cercedilla*", dominado por claros en pinares. d) Transecto de "*Bola delMundo*", caracterizado por el matorral de alta montaña. Fotografías: Javier Gutiérrez Illan y Robert J. Wilson

Objeto de estudio: Las mariposas de la Sierra de Guadarrama

Los invertebrados constituyen uno de los indicadores biológicos más importantes para la detección y evaluación de cambios ambientales, tanto naturales como antrópicos (Thomas, 2005). Por su parte, las mariposas han demostrado ser organismos ideales para el estudio de los efectos del cambio climático debido a su condición de animales poiquilotérmicos, cuyo ciclo de vida se ve altamente influenciado por el clima y la estructura de la vegetación (Dennis, 1993; Stefanescu et al., 2003; Roy & Asher, 2003). En latitudes templadas, se han llevado a cabo numerosos estudios en los últimos años, basados en éstos organismos y sus respuestas ecológicas frente a los aumentos de temperatura (por ejemplo, White & Kerr, 2006; Araújo & Luoto, 2007; Pöyry et al., 2009), aunque los estudios de este tipo en la Península Ibérica son mucho más escasos (pero véase Stefanescu et al., 2003).

Por su parte, como ya se ha indicado anteriormente, la Sierra de Guadarrama es una región de una alta diversidad lepidopterológica, donde se encuentran representadas las principales familias de ropalóceros de Europa. En ella encontramos especies presentes en las listas de protección legal y libros rojos nacionales y europeos que son muy importantes desde el punto de vista de la conservación, como *Parnassius apollo*, especie emblemática y protagonista de numerosos planes de conservación (Figura 4a) o *Hamearis lucina* (Figura 4b), única especie de la familia *Riodinidae* presente en el continente europeo y que tiene su límite de distribución meridional en esta zona. Aparte de esta última especie, en la Sierra de Guadarrama habitan otras muchas, que tienen su límite latitudinal sur de distribución en Europa en esta región, de manera que sus poblaciones representan las más meridionales del continente (Gómez de Aizpúrua 1987; Kudrna 2002; García-Barros et al., 2004; Wilson et al., 2005). Entre ellas se podrían destacar algunas con poblaciones relativamente abundantes como *Lycaena virgaureae* (Figura 5a), *Coenonympha arcania* (Figura 5b) y *Erebia triaria* (Figura 5c) y que hemos encontrado durante las campañas de campo de ésta tesis.

Figura 4a Ejemplar macho de *Parnassius apollo* en el transecto de "Maliciosa menor", una de las localidades de muestreo situadas a mayor altitud. Fotografía: Roberrt J. Wilson.

Figura 4b Ejemplar de *Hamearis lucina* en las proximidades del transecto de "Rascafría", durante el mes de Mayo de 2007. Fotografía: Javier Gutiérrez Illán.

Durante los muestreos de campo de esta tesis se contabilizaron un total de 102377 individuos repartidos en 132 especies, registrándose 21831, 16844, 26239, 21455 y 16008 individuos en los años 2004, 2005, 2006, 2007 y 2008, respectivamente. Debido a las dificultades de identificación en el campo, las especies de los géneros como *Pyrgus*, *Carcharodus* o *Mellicta*, no se pudieron separar y se trataron como una sola unidad en los análisis posteriores.

La prevalencia relativa (proporción de localidades ocupadas) de las 70 especies presentes en todos los años de muestreo estuvo fuertemente correlacionada entre años ($r_s > 0.71$, $P < 0.001$, $n = 70$, en todos los casos)

Figura 5a *Lycaena virgaureae* en las proximidades del transecto de “Valle Enmedio”. Fotografía: David Gutiérrez.

Figura 5b *Coenonympha arcania* en las proximidades del transecto de “Pinilla I”. Fotografía: David Gutiérrez.

Figura 5b *Erebia triaria* en el transecto de “El Palancar”. Fotografía: Robert J. Wilson.

Introduction

Background

Global climate change and habitat loss now represent the main threats to biodiversity (Wuethrich, 2000, Parmesan & Yohe, 2003; Root el at., 2003). These changes include not only temperatures, which have shown marked rises of 0.6ºC in the last 100 years (Houghton, 1996; Gian-Reto et al., 2003), mainly in the second half of the past Century (IPCC, 2007), but also mass melting of terrestrial ice sheets, rise of mean sea level or frequency of extreme climate events like hurricanes and floods, among others. The aforementioned processes could be exacerbated according to the most pessimistic forecasts of the IPCC. However, regional changes which are spatially heterogeneous are much more representative for evaluating responses of organisms, populations and ecological communities to global change (Hughes, 2000; Walther et al., 2003).

The effects of climate warming on biological systems can be diverse and may also interact with some other determinants of change, like habitat fragmentation or land use changes (Thuiller et al., 2004). However, the majority of evidence of these effects in the present literature are those related to shifts in species distributions and changes in phenology patterns of species (Wilson et al., 2007a).

Shifts in species distributions

Evidences of recent changes in distributions

There is widely documented evidence of changes in species distributions (Huntley et al, 1995; Thomas et al., 2004; Guisan & Thuiller, 2005; Araújo & Luoto, 2007) and richness (Stefanescu et al., 2004; White & Kerr, 2006; Marmion et al., 2009) caused by global warming, and even in some cases with the extinction processes of species (Easterling, 2000).

Some of these changes have led to latitudinal and altitudinal shifts in the geographic ranges of species (Parmesan et al., 1999; Parmesan & Yohe, 2003; Hickling et al., 2006). As a result, ecological communities have become increasingly dominated by species associated with warm conditions (Chapin et al., 1995; Holbrook et al., 1997; Sagarin et al., 1999; Beaugrand et al., 2002), and species richness has increased at cool Temperate latitudes (Menéndez et al., 2006). However, habitat degradation interacts with climate change to determine landscape-scale species richness and composition. Consequently, large-scale increases in species richness have occurred more slowly than expected from climate change, and wide-ranging generalist species have increased their prevalence at the expense of sedentary specialists, whose range expansions have been impeded by habitat loss and fragmentation (Warren et al., 2001; Julliard et al., 2003; Menéndez et al., 2006).

Species ranges might respond more rapidly to climate change in mountainous regions than in lowland landscapes, because mountains often retain comparatively intact habitats, and because steep elevational gradients allow species to track changing climates over relatively short distances. The elevational ranges of many species have shifted uphill in conjunction with recent warming, with extinctions at low elevations and colonizations higher up (Pounds et al., 1999; Hill et al., 2002; Peñuelas & Boada, 2003; Franco et al., 2006). However, it is also possible that high mountain regions might suffer the effects of global change in a pronounced and irreversible way (Fielding et al., 1999), since the species living at high elevations have a limited space to shift their distributions uphill in search of cooler temperatures (Wilson et al., 2005) and colonizations by lowland species might fail to compensate for the loss of mountain species to progressively higher elevations (Wilson et al., 2007b). This is because, in numerous cases, the altitudinal shift is not possible because higher locations are already occupied or there is no higher habitat any more (Körner et al., 2007). Therefore, in the most mountainous regions of Europe, like the Iberian Peninsula, the habitable area of these high-elevation species is particularly being reduced due to recent global warming. However, although there is sufficient evidence of changes in distribution due to climate change at the high latitude limits of species in temperate regions (Thomas et al., 2006), studies of this kind are much more scarce in the areas where retractions of species distributions are likely to occur, like warm elevational and latitudinal range limits. One of the main aims of this study is to evaluate changes in the altitudinal distribution of the butterfly populations of the Sierra de Guadarrama, a mountainous region which has recently suffered from the effects of climate change. Important retractions of range margins are expected for these populations.

Predictive ecological modelling

The different scenarios proposed by General Circulation Modes (GCMs) predict higher rises in mean temperatures for the coming decades than occurred during the twentieth century (IPCC, 2007). Therefore evaluating the possible consequences of these rises on biodiversity represents an important challenge. As a result, geographical ecological modelling has gained importance among disciplines in ecology. These models are usually expressed first as verbal hypotheses and then as mathematical equations (Johnson & Omland, 2004), which are developed to predict the probability of occupancy or abundance of individuals or species, based on environmental variables related to climate and land cover variablity, among other variables (Guisan & Zimermann, 2000; Johnson & Omland, 2004). Although the ecological basis of these techniques is well known and part of classic ecology, through the development of new statistical techniques and Geographical Information System (GIS) applications, geographical modelling is becoming one of the most active disciplines in current ecology. Such models are predominantly statistical and probabilistic in nature, since they relate current geographical distributions of species to present environment. However, a wide array of techniques is in continual development. In many cases, species have not been sufficiently studied so far in terms of their dynamic responses to changes in the environment (Woodward & Cramer, 1996; Guisan & Zimermann, 2000). For these reasons, modelling ecological processes like changes in distribution (Pearson & Dawson, 2003; Bradley & Fleishman, 2008; Araújo & Luoto, 2007) and species diversity (White & Kerr, 2007; Nogués-Bravo et al., 2008) is currently at the top of the agenda, and has shown a remarkable development in recent years, as climate change and habitat loss have been revealed as the main causes of changes to species distributions and diversity.

It has recently been argued that the relative importance of different types of variables in geographical modelling depend on the spatial resolution where the study is carried out (Thuiller et al., 2004; Pearson et al., 2004; Gutiérrez Illán et al., *in press*). In the current literature, it is commonly assumed that, at large spatial scales, species richness and distribution are determined mainly by topoclimatic factors while, at regional or local levels, habitat and land use variables become more important (Rahbek & Graves 2001; Thuiller et al, 2004; Luoto et al., 2007). However, in highly mountainous regions, where the climatic conditions vary markedly over short distances and along elevational gradients, the predictive ability of pure topoclimatic models remains unknown. The present study deals with these questions, applying several modelling techniques on time-series data describing the most important aspects of the ecology of the Lepidoptera fauna at a regional scale, in the Sierra de Guadarrama.

Changes in phenology patterns of species

Besides geographical changes in species distributions, current climate change has caused temporal alterations in life cycles of numerous organisms. According to several recent studies, changes in the phenology of species are one of the most powerful tools for detecting and evaluating the effects of climate change on biodiversity (Peñuelas & Filella, 2001; Walther et al., 2002; Peñuelas et al., 2002). Most of these studies report changes in physiological and ecological processes of species (Parmesan & Yohe, 2003; Root et al., 2003), such as advances in appearance and mean flight dates of adult insects accompanying rises in temperature (Roy & Sparks, 2000; Forister & Shapiro, 2003). These effects, mirrored in a temporal dimension also have a spatial component in latitudinal and altitudinal gradients (Wilson et al., 2007a). For example, emergence and flight seasons of insects may be delayed at higher altitudes and latitudes due to lower temperatures in these regions (Gutiérrez & Menéndez, 1998; Bird & Hodkinson, 1999; Fielding et al., 1999; Roy & Asher, 2003). However, in the case of some insects, these phenological delays driven by climate, can be reduced by local adaptations related to suitable site selection or modifications in their life cycles (Thomas, 1993).

To examine the potential changes in phenology patterns associated with climate warming, we need time series data covering the most important aspects of life cycles of study populations. This sort of data are relatively common in several countries in the north of Europe (e.g. Butterfly Monitoring Scheme in the United Kingdom and similar schemes in the Netherlands and National Butterfly Recording Scheme in Finland (Saarinen et al., 2002)), but much less frequent at lower latitudes (but see the case of the Catalan Butterfly Monitoring Scheme, CBMS in the north east of Spain (Stefanescu et al., 2000). Besides, in these databases there is usually a lack of records from mountain regions. As a result, the information about geographical variability of changes in phenology patterns is very limited (although the CBMS currently includes locations in the Pyrenees). The present thesis tries to solve these deficiencies investigating the changes in phenology of butterflies over an elevational gradient in The Sierra de Guadarrama mountain range.

Main aims and structure of the thesis

The main aim of the thesis is to examine the potential changes in distribution, diversity and phenology of species in a mountain range where many species have their lower or “warm” latitudinal range limits. To carry out this study, we selected the butterfly populations of the Sierra de Guadarrama (central Spain) as the study system, because of the high sensitivity of these insects to environmental change, and because of the biogeographical characteristics of this mountainous region (see Methods section for further details). In addition, we aimed to develop specific tools for predicting possible effects of ongoing climate change on the butterfly populations of the region, based on current forecasts of General Circulation Models (GCMs) (IPCC, 2007)

The specific objectives are:

1.-To investigate if the geographical and/or elevational distribution of the butterflies of the Sierra de Guadarrama have changed since 1967-73, and to determine if these changes are consistent with climatic variation in the region during the same period.

2.-To examine whether it is possible to predict the distribution, richness and composition of butterfly species of the Sierra de Guadarrama using models based on topoclimatic and land cover data, coming from different sampling sites located over an elevational gradient.

3-.To investigate the phenology patterns of butterfly populations of the Sierra de Guadarrama along an elevational gradient and over a five-year period (2004-2008), and to detect the possible causes of variation in these patterns.

To fulfil these objectives, the present thesis includes four chapters:

- The **first chapter** describes changes in species distribution accompanying recent climate warming, and evaluates the shifts of population range limits and the consequences of reduced habitable area. The results corresponding to the comparison between the period 1967-73 and 2004 have been published in the journal *Ecology Letters*. In addition this first chapter includes data and results from 2005.

-The **second chapter** comprises the development and evaluation of species distribution and abundance models from environmental information and field data, and tries to determine the relative importance of topoclimatic and land cover factors with regards to their predictive ability. This chapter is accepted and currently in press in the journal *Global Ecology and Biogeography*.

-The **third chapter** deals with the development of species richness and composition models of species, evaluating again the relative importance of topoclimatic and land cover factors. This chapter is currently under review in *Journal of Biogeography*.

Finally, the **fourth chapter**, examines the phenological patterns of butterfly populations over an altitudinal gradient in relation to the delay in the date of emergence along the gradient and the determinants of the species-specific variation in that delay.

The results presented herein are of particular interest in the context of basic research but also in conservation biology, since the conclusions derived from this study will help to make decisions about protection programs for threatened species with a more robust basis than those existing in the past.

Methods

Study system: The “Sierra de Guadarrama”

The Iberian Peninsula is one of the regions with the highest insect biodiversity in Europe, and much of this diversity is concentrated in mountain ranges. The butterfly fauna is particularly diverse, including 220 of the 576 species present throughout the continent. However, the majority of studies that focus on Lepidoptera as indicators of climate change have been carried out in the United Kingdom, a region with a relatively poor diversity (e.g. Thomas et al, 2001; Warren et al., 2001). The Sierra de Guadarrama (central Spain) represents, in turn, a hotspot of regional diversity for butterflies (Van Swaay & Warren, 2003; García-Barros et al., 2004), which indicates a great need to investigate and determine the factors generating this diversity. In addition, during the last third of the twentieth century (since 1967-73), mean annual temperature in the Sierra de Guadarrama rose approximately 1.3ºC (Wilson et al., 2005) implying that butterfly populations, which in many cases reach their lower latitudinal limits in the study system, may be significantly altered. For these reasons, the Sierra de Guadarrama represents an ideal mountain system for studying the effects of climate change on butterfly populations over recent decades.

The Sierra de Guadarrama mountain range represents the northern limit of the Madrid province. This system is commonly known as the Sierra de Madrid, a natural region with a singular beauty and high biological diversity. The highest point is the summit of mount Peñalara, at 2430 metres above sea level (Figure 1).

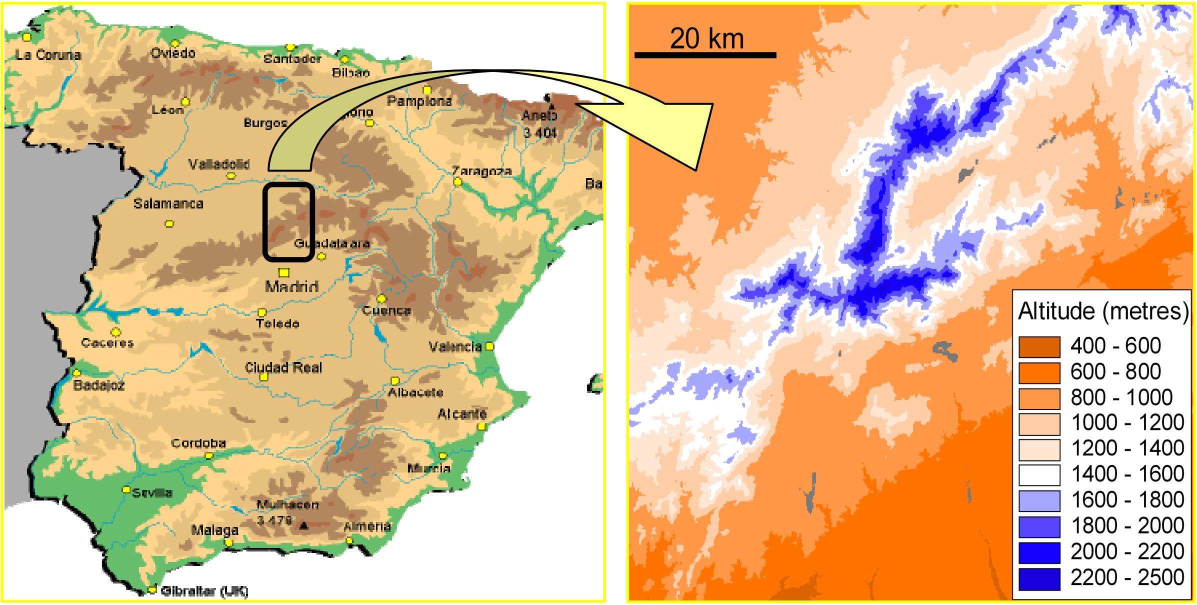

Figure 1 Geographical context of the Sierra de Guadarrama and digital elevation model (DEM) of the study area, showing altitude in elevational bands of 200 metres.

The study area includes 10800 km2 of central Spain, located in a 120 x 90 km grid, running from 40º30’N 4º20’W (UTM reference 30TUK8784) in the south-west to 41º10’N 3º30’W (UTM 30TVL5657) in the north-east. The range is bordered by plains with elevations of ≥535 m (to the south) and ≥700 m (to the north), and includes the Sierra de Guadarram and surrounding areas.

Dominant vegetation types are evergreen broadleaf woodland (largely Quercus rotundifolia) at elevations below 1000 m, deciduous woodland (largely Quercus pyrenaica) at roughly 1000-1500 m, and coniferous woodland (Pinus sylvestris) at approximately 1500-2000 m. Scrub and open grassland are present at all elevations, including beyond 2000 m. (Rivas-Martínez et al., 1987) (Figure 2).

Figure 2 Starting point of transect “La Pedriza” (1050 m.). Sampling area characterized by open pastures and scrubs, located in the southern sector of the Sierra de Guadarrama. Photo: Javier Gutiérrez Illán.

The climate of the study area is continental Mediterranean, and is characterized by a wide thermal variability during the year and by summer drought. The marked elevational gradient is also an additional source of climatic variation, with minimum temperatures below -15ºC in the higher locations and maxima above 35ºC in the lowlands. Rainfall differs also along the gradient and may fluctuate between 700 and 2500 mm.

The information obtained comes from a set of locations with different microclimatic conditions, elevation, population structure and use of habitat by the insects, and was used to determine and evaluate the responses of species to changes in environmental conditions. In order to achieve the main aims of the thesis, two main types of data were used. First, butterfly data obtained in standard linear transects during field surveys and on the other hand, data covering the environmental variation of the study area. Field data came, in turn, from two different surveys. The first survey was carried out during 1967-73 by Victor J. Monserrat in the Sierra de Guadarrama and surrounding areas (Monserrat, 1976). This is a time-series dataset (eight years) of butterfly abundance collected during the flight period of the insects. These data are of an exceptional value, because old observational datasets on butterfly abundance are extremely rare in the Iberian Peninsula. However, it is worth noting that the sampling effort was less controlled than in the current surveys. The second set of field data was collected by the research group in the same sampling area, during 2004-2008. These five-year data were treated independently and have been used in all the thesis chapters. Data on the environmental variation of the study system was collected from meteorological stations in different parts of the region, digital elevation models (DEMs), and vector GIS layers of land cover, generated from different sources (mainly aerial and satellite imagery). Land use, hydrology and geology data, necessary for the characterization of sampling locations, were obtained from these layers.

Sampling locations were accessible open areas of natural or semi-natural habitat, stratified by altitude. The main habitats represented in the transects were pastures and shrublands (Figure 3a), oak woodland clearings (Figure 3b), pine woodland clearings (Figure 3c), and alpine meadows (Figure 3d). Butterfly populations were sampled through standard linear transects (500 m) (Pollard & Yates, 1993), recording butterfly individuals inside a 5x5 m area (5m in front and 2.5 m on both sides of the researcher). These recordings were conducted during the flight season of butterflies every two (phenology transects) or three weeks (rest of locations), between April and October in 2004-2006 and between March and October in 2007-2008 (Table 1).

Table 1 Summary of field surveys according to their contributions to each chapter. The number of locations and the main aim of each chapter is also shown.

	survey (sampling years)	number of locations	main aim
Chapter I	1967-73 / 2004-2005	66 / 180	Temporal changes in distribution of species
Chapter II	2004, 2005	180	Distribution and abundance modelling
Chapter III	2004, 2005	180	Richness and composition modelling
Chapter IV	2004, 2005, 2006, 2007, 2008	20 (2004-2005), 34(2006) 40 (2007-2008)	Phenology patterns in elevational gradients

Figura 3 Some of the sampling transects in the Sierra de Guadarrama. a) Transect "*La Pedriza*", dominated by pastures and shrulands; b) Transect "*El Palancar*", dominated by oak woodland clearings; c) Transect "*Cercedilla*", dominated by pine woodland clearings ;d) Transect "*Bola delMundo*", characterized by alpine meadows. Photos: Javier Gutiérrez Illan and Robert J. Wilson

Study organisms: The Butterflies of the Sierra de Guadarrama

Invertebrates represent one of the most important biological indicators to detect and evaluate environmental changes, both natural and anthropogenic (Thomas, 2005). Besides, butterflies have been demonstrated to be highly sensitive to local climate and vegetation structure, which renders them useful indicators of climate change (Dennis, 1993; Stefanescu et al., 2003; Roy & Asher, 2003). In temperate regions, several studies have recently been carried out based on these organisms and their ecological responses to rises in temperature (e.g. White & Kerr, 2006; Araújo & Luoto, 2007; Pöyry et al., 2009). However, much fewer studies have focused on the effect of climate warming on these insects in the Iberian Peninsula (but see Stefanescu et al., 2003).

As already mentioned, the Sierra de Guadarrama represent a hotspot of regional diversity for butterflies, and it contains most of the families of European Rhopalocera. In this region we find many species present in national and international red lists of threatened species, which are very important in the context of conservation, like the emblematic *Parnassius apollo* (Figure 4a) or *Hamearis lucina* (Figure 4b), the only species from the family Riodinidae that occurs in Europe. Apart from these species, the Sierra de Guadarrama is inhabited by many other species at their lower latitudinal limit, being the southernmost populations in Europe (Gómez de Aizpúrua 1987; Kudrna 2002; García-Barros et al., 2004; Wilson et al., 2005). Among these, there are some species that were relatively abundant in the field surveys, such as *Lycaena virgaureae* (Figure 5b), *Coenonympha arcania* (Figure 5b) and *Erebia triaria* (Figure 5c).

Figure 4a Male individual of *Parnassius apollo* recorded in the transect “Maliciosa menor”, one of the highest sampling locations Photo: Robert J. Wilson.

Figure 4b Individual of *Hamearis lucina* in the surrounding areas of the transect “Rascafría”, in May 2008. Photo: Javier Gutiérrez Illán.

A total of 102377 individuals of 132 species were recorded during the field surveys of the present study. We recorded 21831, 16844, 21455 and 16008 individuals in 2004, 2005, 2006, 2007 and 2008, respectively. Because of identification problems in the field, we were not able to distinguish the individuals of three genera (*Carcharodus, Mellicta* and *Pyrgus*), so we pooled the species in each of these three genera for further analyses.

The relative prevalence (proportion of sites occupied) of the 70 species present in all annual surveys was strongly correlated between years (rs > 0.71, P < 0.001, n = 70, in all cases).

Figure 5a *Lycaena* virgaureae in the surrounding area of transect "Valle Enmedio". Photo: David Gutiérrez.

Figure 5b *Coenonympha arcania* in the surrounding area of transect "Pinilla I". Photo: David Gutiérrez.

Figure 5c *Erebia triaria* in the transect "El Palancar". Photo: Robert J. Wilson

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CAPÍTULO I: Changes to the elevational limits and extent of species ranges associated with climate change

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Cover photograph: Transect “El Berrueco”, in the north-east sector of the Sierra de Guadarrama. Photo: Javier Guiérrez Illán.

ABSTRACT

The first expected symptoms of a climate change-generated biodiversity crisis are range contractions and extinctions at lower elevational and latitudinal limits to species distributions. However, whilst range expansions at high elevations and latitudes have been widely documented, there has been surprisingly little evidence for contractions at warm margins. We show that lower elevational limits for 16 butterfly species in central Spain have risen on average by approximately 200 m in 30 years, accompanying a 1.3ºC rise (equivalent to ≈225 m) in mean annual temperature. These elevational shifts signify an average reduction in habitable area by one third, with losses of 50-80% projected for the coming century, given maintenance of the species' thermal associations. The results suggest that many species have already suffered climate-mediated habitat losses that may threaten their long-term chances of survival.

Keywords Conservation, extinction, Lepidoptera, range margins, range shifts, species distributions, elevational associations

INTRODUCTION

Climate change is expected to force species distributions towards higher elevations and latitudes, leading to extinctions when future habitable climate space is too small or too isolated from species' current geographical ranges (Hill *et al.* 2002; Midgley *et al.* 2002; Thomas *et al.* 2004; Williams *et al.* 2004). However, whilst many species distributions have expanded at their cool, upper elevational and latitudinal margins in conjunction with recent warming (Grabherr *et al.* 1994; Parmesan 1996; Parmesan *et al.* 1999; Pounds *et al.* 1999; Thomas & Lennon 1999; Warren *et al.* 2001; Hill *et al.* 2002; Klanderud & Birks 2003; Konvicka *et al.* 2003; Parmesan & Yohe 2003), surprisingly few range contractions have been documented at warm, lower elevational and latitudinal limits (Parmesan *et al.* 1999; Thomas

& Lennon 1999; Hill *et al.* 2002), perhaps because the locations of warm margins are determined by biotic interactions rather than climate *per se* (Davis *et al.* 1998; Loehle 1998; Pearson & Dawson 2003), or because the mechanisms that cause extinctions are not instantaneous (e.g., sporadic extreme climatic events; Pounds *et al.* 1999; Easterling *et al.* 2000; Parmesan *et al.* 2000; McLaughlin *et al.* 2002). Alternatively, spatial scales of recording or historical information may have been too imprecise to identify declines at lower latitudinal margins, particularly if species have shifted their regional distributions to higher elevations (Parmesan *et al.* 1999; Hill *et al.* 2002; Konvicka *et al.* 2003). Given that many taxa occupy spatially-isolated mountainous regions at their warm margins (Stefanescu *et al.* 2004), such elevational shifts might have the capacity to mask range contractions, constraining species distributions to progressively smaller and less viable population networks until their entire regional persistence is threatened.

Here we document elevational shifts over the last 30 years in the butterfly fauna of the Sierra de Guadarrama (central Spain), a mountain range that represents the lower latitudinal or elevational boundary for many species of butterfly (Gómez de Aizpúrua 1987; Kudrna 2002; García-Barros *et al.* 2004). We propose that the elevational shifts are a response to regional warming, and quantify the effects of changing temperatures on the elevational associations and size of the species' regional distributions. The results provide the clearest evidence for systematic, multi-species contractions at warm range margins in conjunction with recent climate change.

MATERIALS & METHODS

Study system

The Sierra de Guadarrama is a mountain range of c. 100 km, running from 40º30'N 4º20'W (UTM reference 30TUK8784) in the south-west to 41º10'N 3º30'W (UTM 30TVL5657) in the north-east. The range is bordered by plains with elevations of ≥535 m (to the south) and ≥700 m (to the north)(Fig.1).

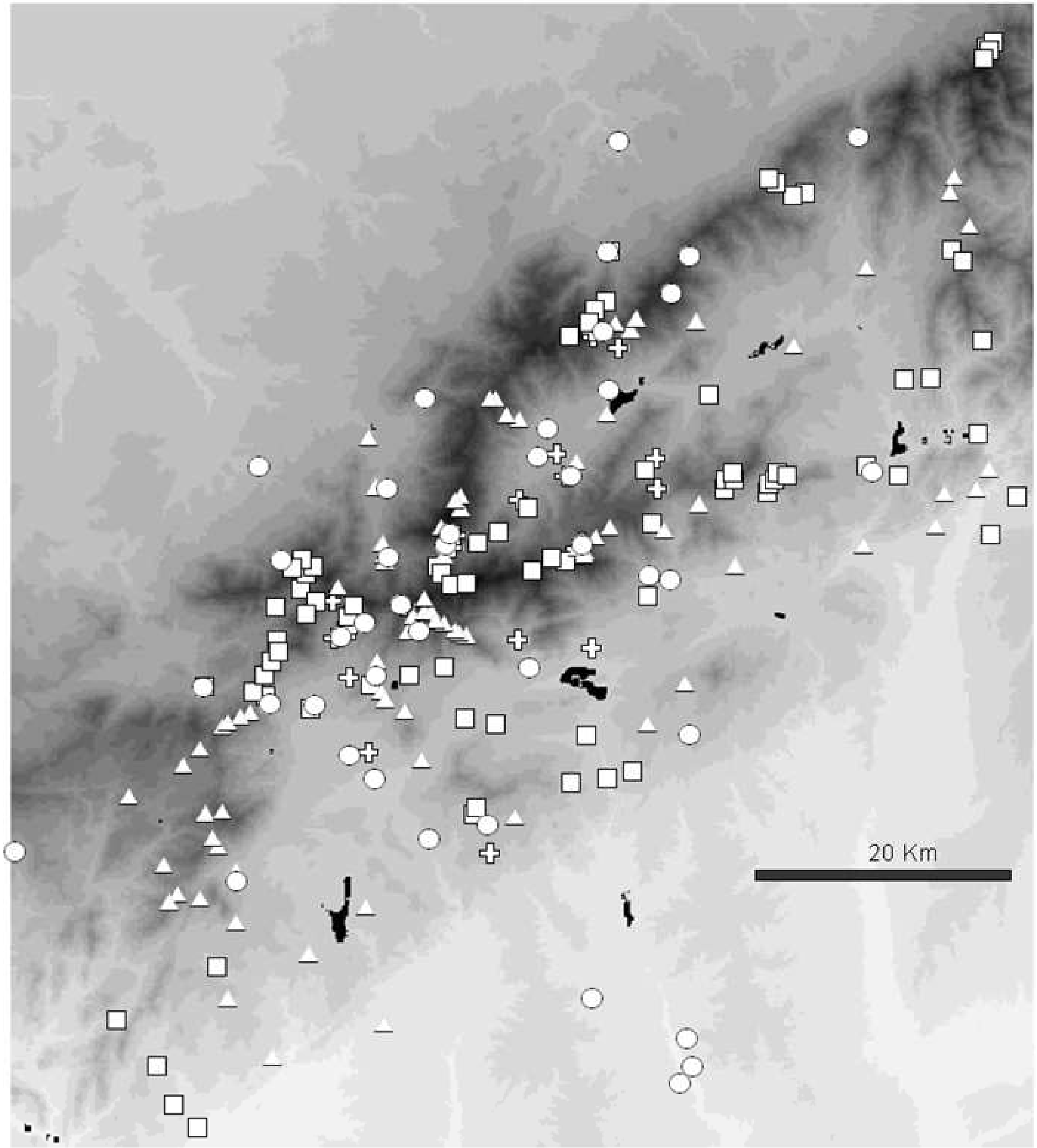

Figure 1 Map of the Sierra de Guadarrama, showing elevation and butterfly sample locations. Elevations (asl): 200m intervals in grey scale (white = minimum elevation <600m ; black = maximum elevation >2400). Sample locations: circles (1967-1973), triangles (2004), squares (2005) and crosses (20 sites, sampled in both years 2004 and 2005).

The elevational associations of butterfly populations were recorded in 1967-1973, 2004 and 2005. From 1967-1973, 66 sites with an elevational range of 620-2040 m above sea level were visited a total of 977 times (Monserrat 1976). In 2004, 100 locations (elevational range 640-2280 m) were visited 539 times in total. In 2005, 103 locations (elevational range 605-2322 m.) were visited 679 times in total. 20 sites were visited both years 2004 and 2005. Survey sites were areas of grassland (pastures, woodland clearings and alpine meadows), stratified by elevation. In 1967-1973, all individuals of all species that were observed during each visit were recorded, but the number of visits to each site and the duration of visits varied. Study sites in 2004 and 2005 were visited every two weeks between April and October (20 locations), or every three weeks between May and August (80 locations). In the 2004-2005 surveys, butterflies were counted on standardized 500m transects (Pollard & Yates 1993) during suitable conditions for butterfly activity. Analysis includes all sites visited in 2004-2005, and the 44 sites visited in 1967-1973 that contained no fewer than 5 species or 13 individuals, the minima recorded for individual sites visited in 2004-2005. Mean distance between nearest neighbouring sites was 2.2 km ± SE 0.2 in 2004 and 1.9 Km ± SE 0.2 in 2005, compared with 6.2 ± 0.8 km for the 44 sites selected for 1967-1973.

Elevational associations were analysed for species with herbaceous or gramineous larval host plants (Tolman & Lewington 1997), and single annual flight periods with peak emergence between May 27th and August 30th, determined by the two-weekly transects. For 1967-1973 data, sites were only included in analysis if they were visited during the annual flight period for each species, in other words between the earliest and latest annual dates of observation for each species in 1967-1973. Species included were non-migratory (Pollard & Yates 1993; Cowley *et al.* 2001), but to avoid including vagrant individuals in analysis, species were considered "present" only if two or more individuals were recorded at a site. Species were "absent" if no individuals were recorded. Sites with one individual were excluded. Analysis was restricted to species that were present in ≥10% but ≤90% of locations. Comparisons were made between 2004 and 2005 to test that differences in elevational associations were not related to very different summers but to long-time processes.

Change in elevational associations

To determine elevational associations in each time period, binary logistic regressions (Norusis 1998) were carried out for presence / absence of each species against elevation (km) and elevation^2. Unimodal models that included a positive effect of elevation and a negative effect of elevation^2 were used to estimate an “optimum altitude” with the highest probability of occupancy for each species.

To test the validity of results based on unimodal logistic regression models, species’ elevational distributions were also fitted to Huisman-Olff-Fresco (HOF) models (Huisman *et al.* 1993; Oksanen & Minchin 2002). HOF models allow testing of alternative responses to ecological gradients (skewed, symmetrical, plateau, monotone), using the model for probability of occupancy $(P) = 1 / (1 + \exp (a + bx)) (1 / (1 + \exp (c - dx)))$, where the x variable was elevation, scaled between 0 (for the lowest elevation datapoint) and 1 (for the highest elevation datapoint). Potential HOF distribution models are: V) skewed, including parameters a-d; IV) symmetric, including parameters a-c, and parameter d = parameter b; III) plateau, including parameters a-c, parameter d = 0; II) monotone, including parameters a-b. Freely available software (Oksanen 1996) was used to fit HOF models for the probability of species occupancy against elevation. The software used a binomial error term and backwards stepwise selection for the most parsimonious model for presence / absence that did not result in a significant change in deviance ($P < 0.05$).

To compare species’ lower and upper elevational limits between surveys, 2004 and 2005 sampling locations were divided into 200 m elevational bands (600-799, 800-999 m etc.), and ten random sets of 44 locations were selected with the same number in each band as in 1967-1973. Change in minimum or maximum elevation for each species was the mean difference between 1967-1973 and the ten random samples from 2004 and 2005. Species that were recorded from the lowest elevation sites in 1967-1973 (620 m elevation) and the lowest elevation site in each random sample from 2004 (640 m elevation) and 2005 (605 m elevation) were not considered to have increased or decreased their lower elevational limits.

Changes in elevational limits could be caused by changes in the status of species: expanding species might have colonized both higher and lower elevations than before; declining species might have disappeared from both high and low elevations (see Thomas & Lennon 1999; Hill *et al.* 2002). Thus, if most species were declining, lower elevational limits would be expected to increase irrespective of shifts in elevational associations. To control for these effects, we regressed change in minimum and maximum elevation against change in occupancy between surveys: the intercepts of these regressions indicate whether elevational limits have generally shifted, independent of changes in occupancy. Occupancy change was the proportion of locations occupied in 1967-1973, subtracted from the mean proportion occupied in the ten random samples from 2004 or 2005, divided by the proportion occupied in 1967-1973. For cross-species analyses of changes in elevational limits (or modelled habitable area, below) against occupancy change, we used the freely available software package COMPARE (Martins 2004) to run phylogenetic generalized least squares (GLS) regressions (Martins & Hansen 1997), with a butterfly phylogeny based on those presented in Harvey (1991) and Cowley *et al.* (2001).

Change in habitable area

A digital elevation model was obtained (NASA/JPL Caltech 2004) for an 80 x 80 km square centred on the Sierra de Guadarrama (UTM co-ordinates SW corner 30TUK8575, NE corner 30TVL6555, see Figure 1). The probability of occupancy for each species based on the elevation of each 100 x 100 m cell in the region was modelled in ArcView GIS (Environmental Systems Research Institute 1996) using the logistic regression or HOF models based on the species' elevational associations in 1967-1973 and in 2004 and 2005.

Proportion change in area with modelled probability of occupancy ≥10%, ≥20%, and ≥50% was calculated for each species as modelled area in 1967-1973, subtracted from area in 2004 or 2005, divided by area in 1967-1973. In order to estimate the average change in habitable area between the two surveys, independent of changes in the proportion of locations where species were recorded (that could depend on changes in sampling intensity at different altitudes), change in modelled area was regressed against occupancy change between the surveys. Occupancy change was the proportion of locations occupied in 1967-1973, subtracted from the proportion occupied in 2004 or 2005, divided by the proportion occupied in 1967-1973.

Change in regional climate

We tested how climate had changed at meteorological stations in the Sierra de Guadarrama between the initial survey (1967-1973) and the same time period immediately preceding the 2004 and 2005 surveys (1997-2003). Meteorological stations were selected with complete records for 1967-1973 (13 temperature stations, 21 rainfall) or 1997-2003 (ten temperature stations, 11 rainfall). Mean annual temperature or rainfall were regressed against elevation (km).

Thermal associations of species ranges

The linear regressions of mean annual temperature against elevation for 1967-1973 and for 1997-2003 were used to model mean temperature at each butterfly sample location in each time period. Logistic regressions for presence / absence were repeated, substituting mean annual temperature for elevation. These logistic regression models were then used to predict the probability of occupancy of each butterfly at each sample site in each time period, based on the species' temperature associations in the other time period (i.e. thermal associations in 1967-1973 were used to predict distributions in 2004, and vice versa). For species whose temperature associations significantly predicted their distributions between the two time periods ($P < 0.05$ both predicting forwards from 1967-1973 and backwards from 2004), the regional area of climatically-suitable habitat was then modelled, based on further increases in mean annual temperature of 1ºC (equivalent to mid-range projections for the mid-21st century, or minimum projections for the late 21st century) or 2ºC (equivalent to maximum projections for the mid-21st century, or mid-range projections for the late 21st century) (IPCC 2001). Habitable area was modelled in ArcView GIS as above, by converting elevation to modelled mean annual temperature using the equations: 2004 mean temp. = 18.2ºC – 5.8 X elevation (km); 2004 mean temp.+1ºC = 19.2ºC – 5.8 X elevation (km); 2004 mean temp.+2ºC = 20.2ºC – 5.8 X elevation (km) (see Results, Change in Regional Climate).

RESULTS

Abundance and species richness

The 1967-1973 survey recorded 16698 individuals of 112 butterfly species, the 2004 survey recorded 30253 individuals of 98 species (in addition to three genera that were not identified to species level in 2004) and the 2005 survey recorded 25973 individuals of 105 species. The difference in species richness between the surveys was partly related to the absence of 6 spring-flying species from the 2004 survey, that have been observed in the study area during April / May of 2003 and 2005. Apart from these 6 springtime species, 10 species were observed in 1967-1973 but not in 2004, all of them very rare (29 individuals in total); 2 species were observed in 2004 but not in 1967-1973. 11 species were observed in 2005 but not in 2004 (mainly spring-flying species that were active too early in the year to be detected by the 2004 survey) species and 4 species were observed in 2004 but not in 2005. Overall, relative rarity or commonness of the species was consistent between the surveys. Results were consistent using species abundance (total number of individuals observed), or dividing study sites into 400 m elevational intervals.

Change in elevational associations

Twenty-five species satisfied the criteria for analysis (see Methods, Study System), of which 23 had significant logistic regressions ($P < 0.05$) in the three time periods for probability of occupancy against elevation and elevation^2 (see Table S1 in Supplementary Material). Seven of these species are widespread in central Spain and were found in the lowest 200 m elevational band (600-799 m), whereas 16 of the species have regional distributions that are restricted to higher elevations (Gómez de Aizpúrua 1987; García-Barros *et al.* 2004). One of the high elevation species (Parnassius Apollo) was recorded in less than 10% of the samples during 2005, and is therefore excluded from comparisons between 1967-73 and 2005.

Of the 69 significant logistic regression models, 65 included a positive effect of elevation and a negative effect of elevation^2, producing unimodal curves for probability of occupancy against elevation, with an “optimum elevation” where the species had the highest probability of occupancy (Fig. 2a, b, e). For the nineteen species whose optima in 1967-73 and 2004 fell within the available elevational range (>600 m, <2400 m), mean change in optimum elevation from 1967-1973 to 2004 was +119 m (± SE 63), with a significantly larger number of species showing increases (fourteen) than decreases (five). Results remain consistent for the 2005 data (Table1).

When the same 23 species’ elevational distributions (except *P.apollo,* removed from analysis in 2005) were fitted to HOF models, 34 of the 68 best-fitting models were symmetric and unimodal, twelve were skewed, ten were plateau and twelve monotone (Table S2). For the 13 species whose HOF-modelled optima in the three time periods fell within the available range, optimum elevation increases for most of the species, with significantly more species showing increases than decreases (Table 1).

Table 1 Elavational associations (optimum, maximum and minimum elevations of the target species) and changes in occupancy between the three surveys.

	Mean Change	N species increase	N species decrease	Wilcoxon *Z*	p-value
Opt. elev. (Log Reg)					
1967-73 vs 2004	+119 m (± SE 63)	13	5	-1.97	<0.05
1967-73 vs 2005	+167 m (± SE 77)	14	6	-2.05	<0.05
2004 vs 2005	+52 m (± SE 32)	12	7	-1.45	0.15
Opt. elev. (HOF)					
1967-73 vs 2004	+189 m (± SE 57)	9	4	-2.48	<0.05
1967-73 vs 2005	+186 m (± SE 40)	8	1	-2.19	<0.05
2004 vs 2005	-24 m (± SE 30)	6	6	-0.71	0.48
Min. elevation *					
1967-73 vs 2004	+204 (± SE 46)	12	4	-2.79	<0.01
1967-73 vs 2005	+177 (± SE 46)	12	3	-2.73	<0.05
2004 vs 2005	-6 (± SE 24)	5	10	-0.88	0.38
Max. elevation					
1967-73 vs 2004	+79 (± SE 64)	12	10	-1.02	0.31
1967-73 vs 2005	+129 (± SE 64)	15	7	-2.26	0.05
2004 vs 2005	+ 51 (± SE 24)	18	4	-2.61	0.01
Occupancy					
1967-73 vs 2004	+ 0.16 (± SE 0.16)	11	11	-0.34	0.73
1967-73 vs 2005	+ 0.22 (± SE 0.13)	12	10	-1.15	0.25

* Analysis based on the 16 (2004) and 15 (2005) high elevation species.

Comparison of the high elevation species distributions (>800m) in 1967-73 with the randomly re-sampled 2004 & 2005 data showed that lower elevational limits had increased for most of the species (Table 1).

Referring to the upper elevational limits, there was no significant change in 2004 with respect to the 1967-73 survey. On the contrary, there was a significant change in the 2005 survey in comparison with 1967-73 and also in comparison with 2004 (Table 1). In general, species occupancy did not decline between 1967-73 and 2004-05 (Table 1). For the 16 species that were restricted to high elevations in 1967-73 and 2004 surveys, the regression of change in lower elevational limits against change in occupancy between surveys was significant, with a significant intercept of 212 m ($R^2 = 0.39$, Ln likelihood = -89.86; $P < 0.05$; change (m) = 212 m [± SE 60; $P < 0.05$] – 159 [± SE 53; $P < 0.05$] X occupancy change) (Fig. 3a). Comparing the distributions of the same 15 species (except *P.apollo*) between 1967-73 and 2005, the regression of change in lower elevational limits against change in occupancy was marginally non-significant, with a significant intercept of 195 m ($R^2 = 0.21$, Ln likelihood = -84.97; $0.05 < P < 0.1$; change (m) = 195 m [± SE 50; $P < 0.01$] – 132 [± SE 70; *P ns*] X occupancy change) (Fig. 3d).

Minimum elevations had not changed significantly for the seven species that occupied the lowest elevational band (600-799 m). Controlling for changes to occupancy, upper elevations had not changed significantly for either group of species (Fig. 3b; Table S3). These results remained consistent if one high-elevation species whose distribution size had increased greatly (*Hyponephele lycaon* Kühn) was removed from analysis (Fig. 3, Table S3).

Change in habitable area

The models relating species distributions to elevation were used to calculate the area of the landscape that exceeded 10%, 20% and 50% probabilities of occupancy in each time period (Fig. 2c, d, f). Based on a 20% threshold probability of occupancy from logistic regression modelling, suitable area for 11 of the 16 high-elevation species had declined in 2004 (mean proportional change = – 0.22 ± SE 0.11; Wilcoxon test, $Z = -2.17$, $P < 0.05$) and in 2005 suitable area had also declined for 11 species (mean proportional change = – 0.19 ± SE 0.09; Wilcoxon test, $Z = -1.99$, $P < 0.05$).

For the 2004 data, the regression of change in modelled suitable area against change in occupancy for the 16 high-elevation species had a signficant intercept of – 0.34 (Fig. 3c; R^2 = 0.76, Ln likelihood = 17.12, $P < 0.001$, Change in area = – 0.34 [± SE 0.09; $P = 0.002$] + 0.35 [± SE 0.05; $P < 0.001$] X occupancy change), indicating that a species that had not changed in occupancy between the surveys had suffered a reduction of approximately one third in its area of climatically suitable habitat. In addition, for the 2005 data, the regression of change in modelled suitable area against change in occupancy for the 15 high-elevation species had a signficant intercept of – 0.28 (Fig. 3f; $R^2 = 0.40$, Ln likelihood = 12.96, $P < 0.05$, Change in area = – 0.28 [± SE 0.08; $P < 0.01$] + 0.24 [± SE 0.08; $P < 0.05$] X occupancy change). This signifies that species that still occupied the same proportion of sample locations had suffered a reduction of 34% and 28%, respectively for 2004 and 2005, in habitable area.

Change in area with ≥10% probability of occupancy decreased by 32-37% in 2004 and by 28-34% in 2005 (based on logistic regression and HOF models respectively), while area with ≥50% probability of occupancy decreased by 46-50% in 2004 and by 15-32% using 2005 data (Table S3).

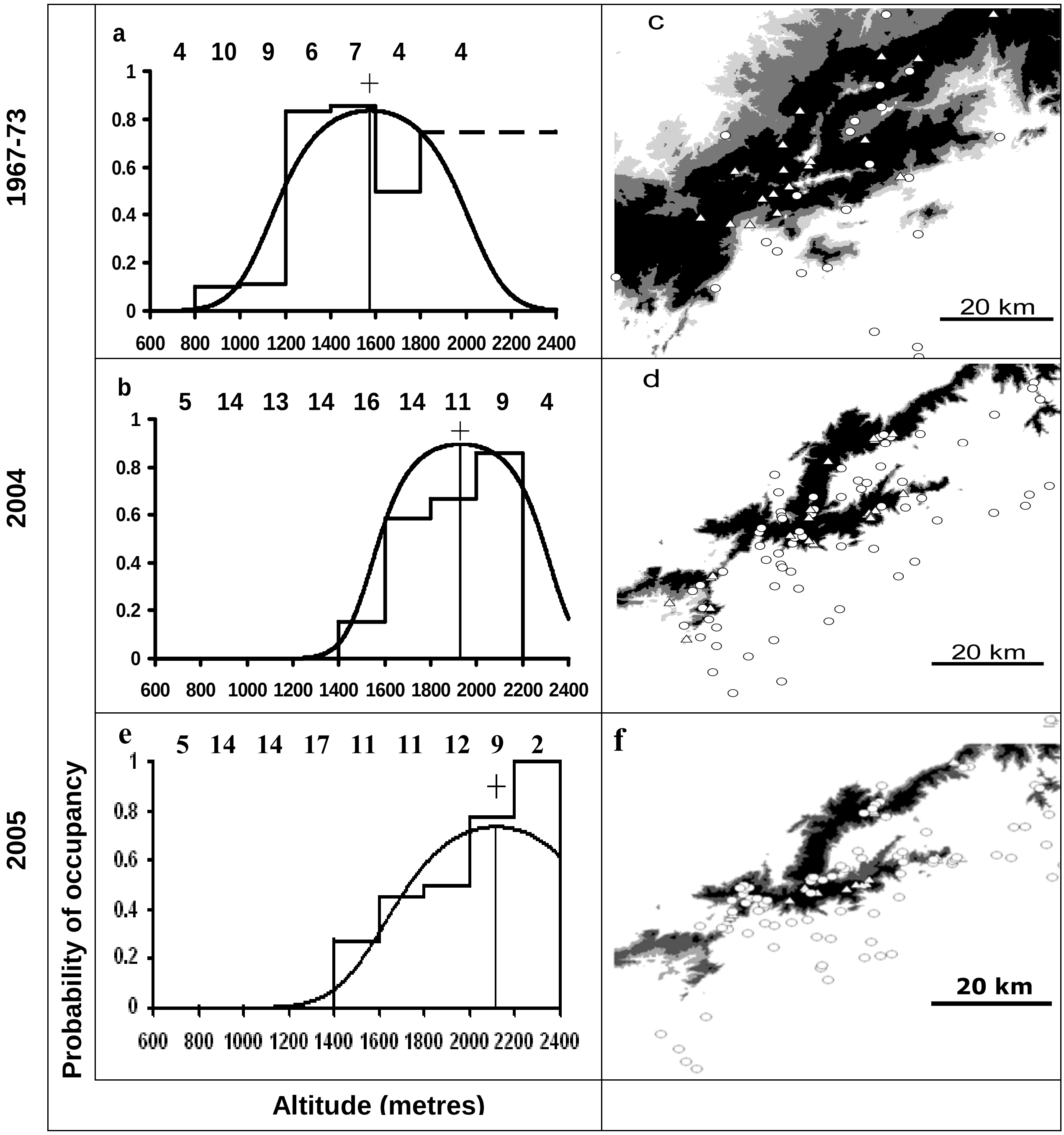

Figure 2 Probability of occupancy at different elevations for the butterfly *Satyrus actaea* Esper. a-b) Histograms of probability of occupancy in 200 m intervals (bars), and probability of occupancy (P) modelled using logistic regression (curve) in a) 1967-1973 [$\text{logit } P = -25.30 + 34.20 \text{ elevation (km)} - 10.86 (\text{elevation})^2$], b) 2004 [$\text{logit } P = -61.69 + 66.12 \text{ elevation (km)} - 17.12 (\text{elevation})^2$] and e) 2005 [$\text{logit } P = -29.76 + 29.12 \text{ elevation (km)} - 6.89 (\text{elevation})^2$]. Crosses show ‘optimum’ elevations with highest modelled probability of occupancy. Number of samples per 200 m interval shown above each bar. In a) dashed line denotes proportion of all four sites sampled above 1800 m., c-d-f) Distributions of suitable elevations based on equations in a), b) and e) respectively, for c) 1967-1973, d) 2004 and f) 2005. Black ≥50% probability of occupancy; dark grey ≥20%; pale grey ≥10%; white <10%. Sample locations: triangles (occupied), circles (vacant).

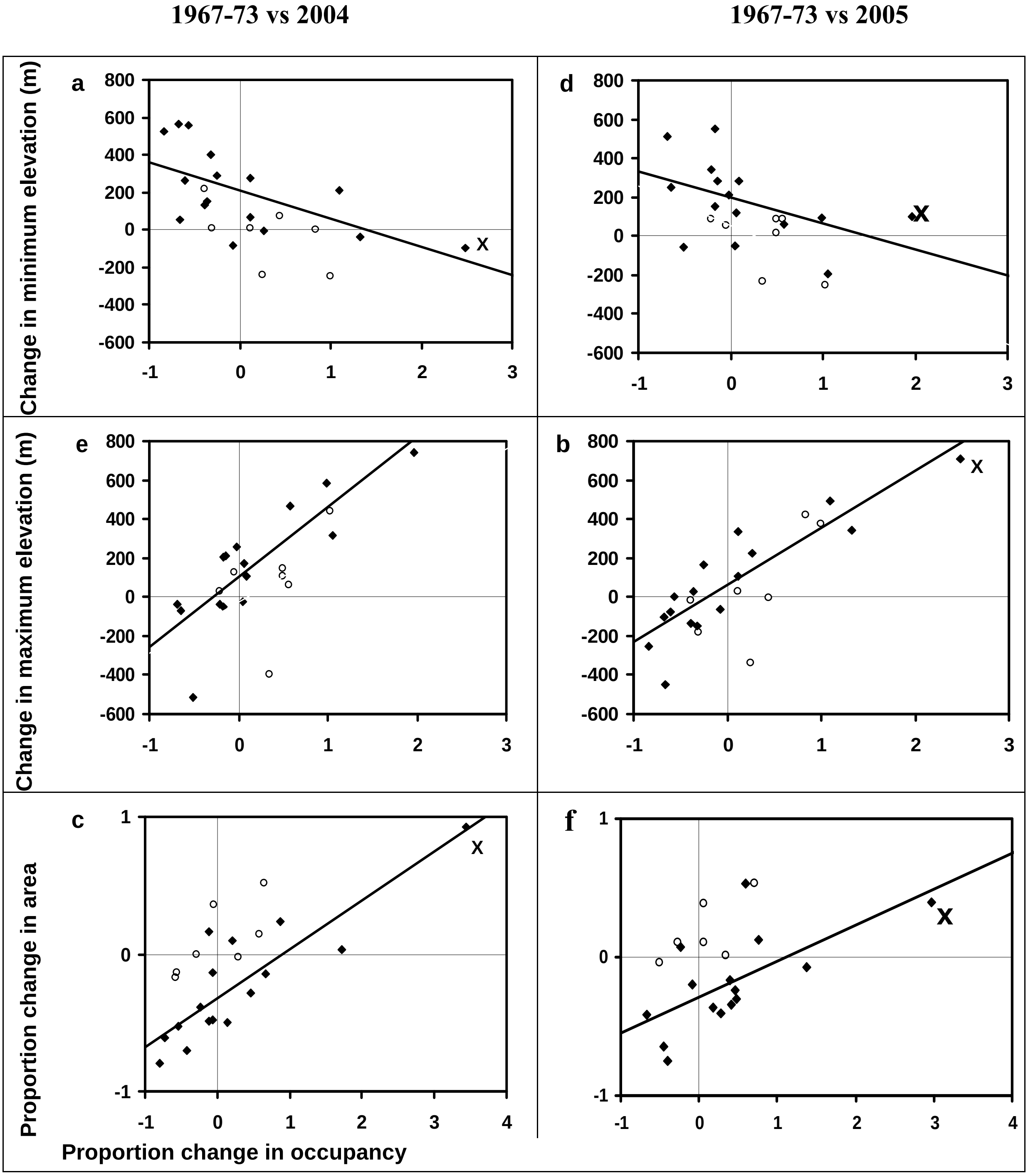

Figure 3 Changes in elevational associations and modelled habitat availability against occupancy change for 1967-1973 vs 2004 and 1967-1973 vs 2005. a,d) Change in lower elevational limit (m); b,e) Change in upper elevational limit (m); c) Proportion change in area with ≥20% modelled probability of occupancy. Species not found below 800 m: solid symbols, regression lines. Species found below 800 m: open symbols, regressions not significant. Full data set used to calculate occupancy change in c), re-sampled data used in a), b). X indicates one outlying species with a greatly increased distribution size.

Change in regional climate

Annual mean temperature decreased by approximately 6ºC per 1000 m elevational increase in each period, but annual mean temperatures in 1967-1973 were 1.3ºC cooler than thirty years later, based on the intercepts of linear regressions of temperature against elevation (Table 2a, Fig. 4). The increase of 1.3ºC indicated a ≈225 m rise in the locations of sites with comparable thermal microclimates (based on a decrease in temperature of 5.8 or 5.9ºC per 1000 m increase in elevation). Changes in temperature between the two periods remained consistent if data from the highest altitude station were excluded.

Mean annual rainfall increased with elevation, but did not change significantly between the two periods (Table 2b).

Table 2 Linear regressions of a) annual mean temperature (ºC) and b) annual rainfall (mm) against elevation (km) for 1967-1973 and 1997-2003.

	R^2	N^*	F	$B_0^\dagger$	±SE	$B_1^\ddagger$	±SE
a) Temperature (ºC)							
1967-1973	0.93	13	155.7***	16.9	0.5	-5.9	0.5
1997-2003	0.94	10	132.6***	18.2	0.5	-5.8	0.5
b) Rainfall (mm)							
1967-1973	0.91	21	180.4***	-32.9	53.2	766.7	57.1
1997-2003	0.94	11	140.1***	-16.3	53.5	683.2	57.7

[*] Number of meteorological stations. [†] Units correspond to units of temperature or rainfall. [‡] Annual temperature or rainfall = $B_0 + B_1$ X Elevation (km). Significance: *** $P < 0.001$.

Thermal associations of species ranges

For the 16 high-elevation species, models predicting distributions either forwards (using 1967-1973 temperature associations to predict 2004 distributions) or backwards (using 2004 temperature associations to predict 1967-1973 distributions) were significant ($P < 0.05$) for 15 species (Table S4). Changes to the distribution of only one species (*Coenonympha arcania* Linnaeus) were unable to be predicted by temperature associations. Using the significant relationships of these 15 species' ranges with mean annual temperature to model the extent of habitable area given a further increase of 1ºC in mean annual temperature (2.3ºC relative to 1967-1973) led to 50-70% declines relative to 1967-1973; an increase of 2ºC (3.3ºC relative to 1967-1973) led to 70-80% declines (Table 3).

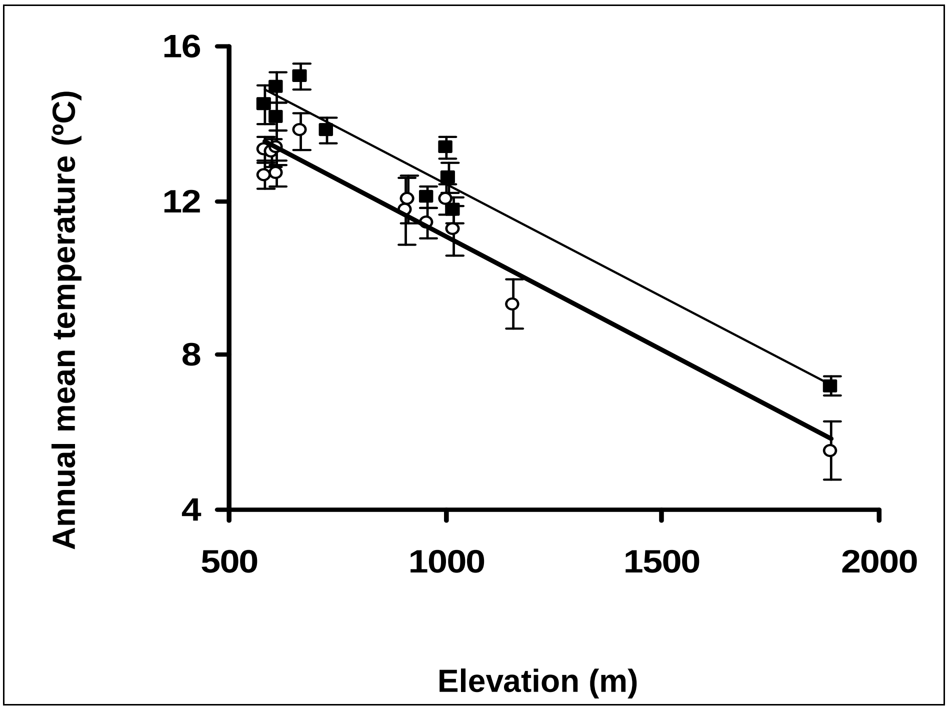

Figure 4 Annual mean temperature against elevation for 1967-1973 (open symbols, thick line) and 1997-2003 (solid symbols, thin line). Symbols represent meteorological stations in the Sierra de Guadarrama. Error bars show 1 standard deviation in annual

Table 3 Projected declines in habitat availability relative to 1967-1973, based on the temperature associations of 15 high elevation species in 1967-1973 and 2004. Models use area of landscape with ≥10%, ≥20% and ≥50% probability of occupancy for each species, given temperature increases of 1.3, 2.3 and 3.3ºC relative to 1967-1973.

Temperature increase (ºC)	Temperature associations	Modelled proportion decline per habitat threshold (mean ± SE)		
		≥10%	≥20%	≥50%
1.3	1967-1973	0.45 (±0.03)	0.46 (±0.03)	0.50 (±0.02)
1.3	2004*	0.23 (±0.12)	0.25 (±0.11)	0.29 (±0.18)
2.3	1967-1973	0.65 (±0.02)	0.66 (±0.02)	0.71 (±0.02)
2.3	2004	0.49 (±0.09)	0.50 (±0.09)	0.51 (±0.13)
3.3	1967-1973	0.79 (±0.02)	0.81 (±0.02)	0.86 (±0.02)
3.3	2004	0.69 (±0.06)	0.70 (±0.06)	0.72 (±0.08)

*For 2004 associations, values for 1.3ºC increase show observed mean decline in area.

DISCUSSION

Change in elevational associations

Over thirty years of regional warming there were pronounced upward shifts in the elevational ranges of the butterflies of the Sierra de Guadarrama. For most of the 23 species of grassland butterfly studied, the optimum elevation (with the highest modelled probability of occupancy) increased from 1967-1973 to 2004 & 2005, with average increases of 120-200 m, depending on the type of model used to relate occupancy to elevation, and the number of species for which the models detected an elevation with a peak probability of occupancy. Increases in optimum elevation appeared to result from extinctions at low elevations rather than colonizations at high elevations. For the 16 species that were restricted to high elevations in the 1967-73, 2004 and 2005 surveys (i.e. species at their “warm” range margins), the increase in lower elevation increased for 11 and 12 species, respectively. Changes in lower limits between 1967-73 and 2004 surveys appeared to be independent of overall changes in occupancy: a regression of change in lower elevational limit against change in occupancy between the surveys suggested that lower elevational limits for these species had increased by 205 m (Fig. 3a). Results were remarkably consistent comparing lower elevational limits in 1967-73 and 2005, with a significant change of 195 m. Upper elevational limits in 2004 only increased for 12 of the 23 species, and change in upper elevational limit was not significant when controlling for the effects of changes in occupancy (Fig. 3b). In contrast, for the 2005 data upper elevational limits had increased since 1967-73 for 15 of the 22 species, and this relationship remain significant when controlling for the effects of changes in occupancy. Upper limits also increased in 2005 either suggesting local colonisations or increases in population density at the highest locations, possibly caused by the hotter and dryer summer in 2005.

Nevertheless it is worth noting that, even though we found an increase in the upper elevational limits between 2005, the losses in habitable area since 1967-73 remained approximately 30% on average, suggesting that the possible increase in habitable area at the top of the mountains does not compensate for the losses at the lower locations caused by the global warming.

Two sources of evidence suggest that the overall patterns observed reflect genuine changes in distribution rather than inter-annual variation in abundance or temporary uphill dispersal associated with weather conditions. As a further test for the role of changes in observed distributions between successive years, we calculated lower and upper elevational limits separately for 1970 and 1971, using the 18 sites which had distribution data from both years: the 23 study species showed minor and non-significant changes in elevational range limits (lower limits, mean change = -17 m ± SE 42; upper limits, mean change = -23 m ± SE 32), even though temperature varied by 0.6ºC between the successive years (regressions of mean annual temperature against elevation had intercepts of 17.1 and 16.5ºC for 1970 and 1971 respectively). Second, the 120-200 m shifts in minimum and optimum elevations represent 3-5 km shifts in geographic location, based on an elevational gradient of approximately 40 m per 1 km in the Sierra de Guadarrama. The non-migratory butterflies studied typically move less than a few hundred metres in their lifetime (Pollard & Yates 1993), so the changes almost certainly reflect genuine shifts in distributions to higher elevations, rather than temporary annual dispersal. Whilst making this point it is worth noting that the changes in distributional limits of 3-5 km would be unlikely to be detected at the kind of scales used for regional or national distribution mapping (e.g. 10 km, Warren *et al.* 2001; García-Barros *et al.* 2004).

Causes for elevational range shifts

The apparently systematic elevational range shifts suggest a wide-acting and consistent explanatory factor, such as climate. The magnitude of increase in lower elevational limits between the surveys (approximately 200 m for the 16 high-elevation species) was similar to that expected based on change in mean annual temperature (+1.3ºC ≈ 225 m increase). Furthermore, the thermal associations for 15 of the high-elevation species in 1967-1973 significantly predicted their distributions in 2004 (based on temperatures in 1997-2003), and vice versa. Based on changes to lower elevational limits in 2005, it is expected that thermal models for species distributions in 2005 would show similar results.

Nevertheless, the close fit between changing temperatures and changing distributions is not sufficient to demonstrate causation. In some parts of their ranges, despite apparent climatic amelioration, species have declined because of habitat loss caused by land-use changes (Warren *et al.* 2001; Hill *et al.* 2002). In the Sierra de Guadarrama, direct anthropogenic influences on the landscape are likely to have been stronger at low elevations, making it difficult to disentangle the effects of land-use and climate on species distributions. But several sources of evidence point to climate being a more important explanatory factor. The elevational shifts were widespread among a sample of species with ubiquitous larval host plants (Tolman & Lewington 1997), for which large areas of otherwise suitable habitat remain at all elevations (Ministerio de Medio Ambiente 2003). Several of the species that are restricted to high elevations (e.g., *Argynnis adippe* Denis & Schiffermüller, *A. aglaja* Linnaeus, *A. paphia* Linnaeus, *Lycaena alciphron* Rottemburg, *L. virgaureae* Linnaeus) have congeneric species (*A. pandora* Denis & Schiffermüller, *L. phlaeas* Linnaeus) that use the same larval host plants and are common at all elevations, suggesting that the distribution patterns of the localized species are related to their own physiological tolerances or to interactions with the physiological condition of habitat or host plants. At a regional scale, mean annual temperature may capture sufficient variation in annual heat stress or moisture availability to be relatively closely related to the location of the species' "warm" range margins. In contrast, the lack of significant upward shifts in higher elevational limits (when controlling for occupancy) may be related to more specific factors such as extreme winter temperatures (Bale *et al.* 2002; Sinclair *et al.* 2003).

Implications for species distributions and persistence

Even though levels of occupancy for the study species did not change significantly between 1967-1973, and 2004-05, the elevational shifts in species distributions signify a substantial reduction in potentially suitable area for the 16 high-elevation species. When species' elevational associations were used to model regional habitat availability in the three time periods, habitable area had declined on average by approximately 20%. The intercept of -0.34 (2004) and -0.28 (2005) from the regression of change in habitable area against change in occupancy implied that species that still occupied the same proportion of sample locations had suffered a reduction of approximately one third in habitable area, simply because of the smaller area of the landscape at progressively higher elevations.

The significant relationships of 15 high-elevation species distributions with mean annual temperature allowed us to model their likely distribution sizes given projections of climatic warming for the coming century (IPCC 2001). Relatively conservative further increases of 1ºC and 2ºC respectively led to 50-70% and 70-80% declines in modelled habitable area relative to 1967-1973 (Table 2). The Sierra de Guadarrama is bordered to both north and south by lower elevation plains, preventing the northward migration of species range margins, so the projected habitat declines would almost certainly presage regional extinction for many of the species concerned, and for other montane fauna and flora.

CONCLUSION

Elevational shifts by species at their warm margins may prevent the identification of geographic-scale range contractions caused by climate change (Parmesan *et al.* 1999; Hill *et al.* 2002). Despite continuing high levels of occupancy by many species at their warm margins in the Sierra de Guadarrama, species distributions have shifted to higher elevations, implying a reduction in habitable area by one third in only 30 years. These declines in habitable area might themselves be underestimates if there is a time-lag in extinctions from sites that are outside species' long-term climatic tolerance (Hill *et al.* 2002). The regional habitat losses of 50-80% predicted for the next century, given maintenance of the species' climatic associations and continued regional warming, will probably be exacerbated by direct habitat loss through changes in land-use (Warren *et al.* 2001; Stefanescu *et al.* 2004). The magnitude of these declines in available habitat may be typical for species that are restricted to high elevations at their warm range margins (Stefanescu *et al.* 2004), or for endemic taxa that are entirely restricted to mountainous regions (Pounds *et al.* 1999; Williams *et al.* 2003). Given the spatial isolation of suitable high elevations for these taxa, and their consequent inability to colonize new areas as the climate warms (Grabherr *et al.* 1994; Pounds *et al.* 1999; Midgley *et al.* 2002; Klanderud & Birks 2003; Konvicka *et al.* 2003; Williams *et al.* 2003), the results forewarn of widespread extinctions unless climate change and habitat loss can be arrested.

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SUPPLEMENTARY MATERIAL

Additional supporting information may be found in the online version of this article:

Table S1 Logistic regression equations relating butterfly species occupancy to elevation.

a) 1967-1973

Species	N_P	N_A	-2LL	R^2	Chi^2	B_0	B_1	B_2	Optimum elevation (m)
Argynnis adippe	18	25	39.09	0.49	19.38***	-11.18	12.35	-2.79	2213
Argynnis aglaja	14	29	40.94	0.37	13.33**	-27.51	41.72	-15.39	1355
Argynnis paphia	9	33	27.55	0.49	16.10***	-70.83	118.36	-48.98	1208
Coenonympha arcania	9	31	25.23	0.54	17.43***	-51.45	70.70	-23.84	1483
Erebia meolans	7	34	27.12	0.37	10.36**	-6.70	3.08	0.51	>2400
Erebia triaria	12	26	38.17	0.30	9.23*	-17.02	22.54	-7.26	1552
Hesperia comma	13	26	35.63	0.42	14.02**	-29.01	43.03	-15.48	1390
Hipparchia alcyone	8	34	29.53	0.38	11.37**	-54.46	89.10	-36.29	1228
Hipparchia statilinus§	20	20	45.39	0.30	10.06**	-11.64	16.18	-5.04	1605
Hyponephele lycaon	6	34	13.38	0.70	20.44***	-190.38	310.91	-125.9	1235
Kanetisa circe§	17	27	40.63	0.46	18.07***	-21.11	40.36	-18.58	1086
Lycaena alciphron	18	22	42.39	0.36	12.66**	-15.76	21.15	-6.55	1615
Lycaena virgaureae	14	30	41.31	0.38	13.73**	-24.84	34.08	-11.32	1505
Maniola jurtina§	20	23	43.09	0.42	16.31***	2.62	9.29	-5.77	805
Melanargia lachesis§	26	16	48.63	0.21	7.19*	-5.91	12.41	-5.41	1147
Melanargia russiae	12	32	25.74	0.64	25.83***	-63.16	84.83	-27.69	1532
Melitaea cinxia	16	21	43.68	0.23	6.94*	-7.84	14.43	-6.23	1158
Melitaea phoebe§	16	26	43.50	0.35	12.32**	-11.37	22.46	-10.66	1053
Parnassius Apollo	20	24	26.74	0.72	33.90***	-14.51	13.97	-1.73	>2400
Pyronia bathseba§	12	30	40.85	0.29	9.40**	-1.30	4.80	-3.75	640
Pyronia cecilia§	20	23	35.01	0.58	24.39***	-11.98	29.12	-15.69	928
Pyronia tithonus	11	27	29.96	0.49	15.77***	-23.48	47.56	-23.57	1009
Satyrus actaea	18	26	38.96	0.50	20.57***	-25.30	34.20	-10.86	1575

b) 2004

Species	N_P	N_A	-2LL	R^2	Chi^2	B_0	B_1	B_2	Optimum elevation (m)
Argynnis adippe	29	61	88.23	0.34	24.91***	-20.52	24.63	-7.24	1701
Argynnis aglaja	27	61	91.54	0.25	16.97***	-15.81	19.65	-6.04	1627
Argynnis paphia	22	63	83.45	0.22	13.77**	-16.07	20.98	-6.90	1520
Coenonympha arcania	19	76	74.58	0.31	20.50***	-25.58	35.44	-12.34	1436
Erebia meolans	14	79	52.39	0.43	26.41***	-41.16	42.12	-10.78	1954
Erebia triaria	34	61	81.98	0.49	41.94***	-27.48	31.27	-8.58	1822
Hesperia comma	49	39	69.02	0.60	51.83***	-23.89	30.08	-8.66	1737
Hipparchia alcyone	45	42	56.92	0.69	63.59***	-39.81	52.07	-16.00	1627
Hipparchia statilinus§	42	46	71.79	0.58	50.03***	-11.61	23.31	-10.11	1153
Hyponephele lycaon	62	31	58.74	0.66	59.65***	-25.48	33.12	-9.58	1729
Kanetisa circe§	60	34	63.41	0.64	59.62***	-12.26	25.05	-10.40	1204
Lycaena alciphron	32	44	62.07	0.57	41.38***	-32.10	39.71	-11.72	1694
Lycaena virgaureae	43	49	63.88	0.66	63.27***	-40.58	51.14	-15.25	1677
Maniola jurtina§	60	22	59.84	0.51	35.54***	12.41	-10.08	1.72	<600
Melanargia lachesis§	74	18	37.64	0.70	53.31***	-19.02	36.49	-13.49	1352
Melanargia russiae	12	85	54.63	0.32	17.97***	-48.52	58.12	-17.60	1651
Melitaea cinxia	11	82	49.54	0.34	18.07***	-27.51	45.71	-19.31	1184
Melitaea phoebe§	15	75	56.51	0.40	24.59***	-11.53	22.47	-11.06	1016
Parnassius Apollo	9	85	47.51	0.25	11.83**	-40.09	46.12	-13.61	1694
Pyronia bathseba§	19	75	64.39	0.43	30.24***	2.95	-1.88	-1.13	582
Pyronia cecilia§	19	77	31.57	0.77	63.95***	-23.03	59.42	-35.45	838
Pyronia tithonus	50	42	54.49	0.73	72.35***	-23.43	42.49	-17.16	1238
Satyrus actaea	21	68	48.55	0.63	48.70***	-61.69	66.12	-17.12	1931

c) 2005

Species	N_P	N_A	-2LL	R^2	Chi^2	B_0	B_1	B_2	Optimum elevation (m)
Argynnis adippe	35	57	92.15	0.38	30.08***	-21.34	27.21	-8.31	1638
Argynnis aglaja	41	49	90.75	0.41	33.30***	-18.69	23.42	-6.88	1702
Argynnis paphia	35	58	82.71	0.48	40.47***	-29.73	40.09	-12.93	1550
Coenonympha arcania	14	68	79.38	0.40	30.48***	-33.31	44.95	-15.00	1499
Erebia meolans	24	71	57.90	0.60	49.49***	-31.78	31.58	-7.61	2076
Erebia triaria	38	56	81.23	0.52	45.62***	-22.32	25.45	-6.84	1860
Hesperia comma	46	48	75.42	0.59	54.85***	-16.54	18.42	-4.45	2070
Hipparchia alcyone	42	51	69.62	0.62	58.44***	-38.22	48.67	-14.63	1663
Hipparchia statilinus§	47	42	68.08	0.62	56.51***	-2.88	10.51	-5.57	944
Hyponephele lycaon	53	36	39.17	0.81	80.94***	-49.90	63.51	-18.54	1713
Kanetisa circe§	62	32	67.62	0.60	52.95***	9.37	-6.00	0.17	549
Lycaena alciphron	47	41	72.14	0.57	49.44***	-19.98	23.58	-6.32	1864
Lycaena virgaureae	43	53	62.39	0.69	69.65***	-55.39	70.47	-21.36	1650
Maniola jurtina§	42	42	45.59	0.76	70.86***	-0.67	9.67	-6.33	764
Melanargia lachesis§	80	16	38.63	0.66	47.87***	-16.35	32.54	-12.31	1322
Melanargia russiae	15	84	69.67	0.24	14.55***	-15.13	14.33	-3.55	2018
Melitaea cinxia	13	78	51.78	0.40	22.86***	-23.37	42.18	-19.21	1098
Melitaea phoebe§	25	64	73.81	0.43	31.88***	-7.43	15.10	-7.25	1041
Parnassius Apollo	5	92	33.04	0.19	6.36*	-16.09	13.01	-2.93	2223
Pyronia bathseba§	30	69	81.71	0.47	39.74***	-7.80	16.68	-8.29	1006
Pyronia cecilia§	23	75	58.56	0.59	48.24***	-10.07	24.56	-13.79	890
Pyronia tithonus	44	51	81.72	0.54	49.46***	-11.57	22.28	-9.51	1171
Satyrus actaea	23	72	57.30	0.59	47.87***	-29.76	29.12	-6.89	2114

$N_{P/A}$ = N present / absent; -2LL = -2 log likelihood ratio of model. Logit (Probability of occupancy) = $B_0 + B_1$ X elevation (km) + B_2 X elevation^2. Significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. § denotes species observed below 800 m. Optimum elevation is the elevation with the highest probability of occupancy. Nomenclature follows García-Barros *et al.* (2004).

Table S2 Huisman-Olff-Fresco (HOF) models relating butterfly species occupancy to elevation.

a) 1967-1973

Species	Model	Deviance change	df	F	a	B	C	D	Optimum elevation (m)
Argynnis adippe	II	18.96	42	18.72***	3.40	-6.97			>2400
Argynnis aglaja	IV	15.25	41	16.43***	-9.39	15.31	5.30	B	1301
Argynnis paphia	IV	15.63	40	21.38***	-11.18	22.78	7.69	B	1208
Coenonympha	IV	11.46	38	16.00***	-11.68	13.99	7.72	B	1480
Erebia meolans	II	10.35	40	14.12***	4.87	-5.61			>2400
Erebia triaria	II	6.46	37	5.81*	2.50	-3.31			>2400
Hesperia comma	IV	12.94	37	13.24***	-9.15	13.78	5.14	B	1356
Hipparchia alcyone	V	2.99	39	4.36*	-460.62	829.01	5.99	15.53	1398
Hipparchia statilinus§	II	7.34	39	5.87*	1.57	-3.97			>2400
Hyponephele lycaon	V	2.44	37	9.62**	272.57	516.52	12.98	34.57	1349
Kanetisa circe§	IV	11.50	42	11.37**	-5.43	11.72	2.22	B	1083
Lycaena alciphron	II	9.29	39	8.21**	2.09	-4.44			>2400
Lycaena virgaureae	IV	9.11	42	9.07**	-9.49	11.97	5.28	B	1496
Maniola jurtina§	III	6.07	41	6.07*	-540.39	971.39	-0.75		<600-1399
Melanargia lachesis§	IV	5.73	40	4.81*	-4.47	6.94	0.15	B	1093
Melanargia russiae	IV	15.79	42	25.44***	-16.32	20.16	9.57	B	1532
Melitaea cinxia	V	6.22	34	5.47*	-2.35	4.95	18.20	202.6	787
Melitaea phoebe§	III	9.14	40	8.90**	-491.58	882.88	-0.22		<600-1398
Parnassius Apollo	II	33.87	43	50.63***	5.93	-13.81			>2400
Pyronia bathseba§	II	8.62	41	8.01**	-0.89	4.96			<600
Pyronia cecilia§	IV	6.78	41	7.49**	-5.27	12.91	-0.04	B	908
Pyronia tithonus	IV	8.53	36	10.23**	-4.62	13.34	1.78	B	976
Satyrus actaea	IV	6.87	42	7.67**	-11.03	12.63	5.12	B	1528

b) 2004

Species	Model	Deviance change	df	F	a	B	C	D	Optimum elevation (m)
Argynnis adippe	IV	13.44	88	12.95***	-7.38	9.07	4.58	B	1721
Argynnis aglaja	III	16.36	86	15.75***	567.33	-2166.5	0.34		1075->2400
Argynnis paphia	IV	13.99	83	14.38***	-5.97	9.76	4.07	B	1484
Coenonympha arcania	IV	21.62	93	27.57***	-7.80	13.55	5.78	B	1462
Erebia meolans	III	9.32	91	16.62***	703.04	-1333.2	0.54		1513->2400
Erebia triaria	IV	12.87	93	14.19***	-9.91	10.64	5.79	B	1846
Hesperia comma	IV	20.63	86	25.80***	-12.19	12.85	4.92	B	1732
Hipparchia alcyone	IV	48.91	85	69.03***	-14.55	17.29	6.57	B	1642
Hipparchia statilinus§	IV	16.47	86	18.84***	-6.17	11.35	0.46	B	1119
Hyponephele lycaon	IV	24.83	91	40.11***	-16.13	16.14	5.39	B	1733
Kanetisa circe§	IV	24.89	92	36.51***	-9.20	14.48	0.31	B	1179
Lycaena alciphron	V	7.67	73	9.74**	-4.47	5.32	33.63	84.53	1388
Lycaena virgaureae	V	3.67	89	4.89*	-5.14	5.90	18.90	50.45	1404
Maniola jurtina§	II	35.12	81	45.47***	-5.14	7.33			<600
Melanargia lachesis§	IV	30.95	90	70.65***	-16.19	21.25	0.77	B	1302
Melanargia russiae	V	6.64	94	13.13***	-4.02	7.71	2808.7	5716.1	1448
Melitaea cinxia	IV	12.38	91	22.04***	-5.78	15.74	4.52	B	1177
Melitaea phoebe§	V	2.54	87	4.06*	-2.40	9.58	10.00	75.17	927
Parnassius Apollo	V	4.83	91	10.02**	-1.81	4.89	2394.4	4883.5	1447
Pyronia bathseba§	II	30.11	93	42.47***	-1.58	7.61			<600
Pyronia cecilia§	IV	5.16	94	14.40***	-5.87	23.92	-0.55	B	822
Pyronia tithonus	IV	40.52	90	64.55***	-10.84	18.27	2.11	B	1221
Satyrus actaea	V	2.85	86	5.20*	-164.16	185.95	9.02	13.75	2040

c) 2005

Species	Model	Deviance change	df	F	a	B	C	D	Optimum elevation (m)
Argynnis adippe	V	7.03	89	7.19	-4.08	5.52	10.97	30.05	1422
Argynnis aglaja	III	19.87	88	19.78	11.95	-37.65	-0.68	0	1515->2400
Argynnis paphia	IV	36.64	91	39.21	-10.76	14.98	5.62	B	1544
Coenonympha arcania	IV	29.50	98	35.16	-9.10	14.81	6.27	B	1496
Erebia meolans	III	6.43	93	10.93	658.08	-1312.11	-0.34	0	1475->2400
Erebia triaria	IV	9.94	91	11.60	-9.71	9.47	5.02	B	1859
Hesperia comma	II	51.35	93	58.56	4.03	-8.32	0	0	>2400
Hipparchia alcyone	IV	40.80	91	51.72	-15.09	18.07	7.31	B	1669
Hipparchia statilinus§	IV	4.00	87	5.01	-5.79	10.96	-0.84	B	993
Hyponephele lycaon	III	25.48	87	55.52	-25.30	25.47	9.91	B	1719
Kanetisa circe§	II	52.94	93	70.46	-5.66	9.40	0	0	<600
Lycaena alciphron	III	17.98	86	55.52	23.73	-64.58	-1.44	0	1416->2400
Lycaena virgaureae	IV	44.24	94	64.22	-17.88	20.90	9.04	B	1649
Maniola jurtina§	II	68.90	83	110.93	-5.90	12.51	0	0	<600
Melanargia lachesis§	IV	26.71	94	62.37	-17.04	21.46	0.91	B	1323
Melanargia russiae	III	12.16	87	19.49	1744.42	-3718.37	0.79	0	1414->2400
Melitaea cinxia	IV	11.41	89	19.15	-5.45	15.96	3.86	B	1106
Melitaea phoebe§	III	14.25	87	19.49	-3134.61	5649.85	-0.04	0	<600-1555
Pyronia bathseba§	IV	7.34	97	8.42	-4.07	10.82	0.84	B	995
Pyronia cecilia§	V	4.14	95	7.29	-3.61	12.97	178.6	2719.27	723
Pyronia tithonus	IV	17.15	93	18.99	-5.92	11.23	1.11	B	1142
Satyrus actaea	V	5.21	92	8.77	3.21	-4.81	701.2	1454.99	>2400

Model: V – Skewed; IV – Symmetrical; III – Plateau; II – Monotone (curvilinear). Model formula: Probability of occupancy = 1 / (1 + exp (a + bx)) (1 / (1 + exp (c – dx))). x variable is elevation (m), scaled between 0 (for lowest elevation datapoint) and 1 (for highest elevation datapoint). Significance of deviance change: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. § denotes species observed below 800 m.

Table S3 Phylogenetic GLS regressions of change in minimum and maximum elevations, and modelled habitable area, against occupancy change.

a) 2004 vs 1967-73

Dependent variable	Alpha†	R	Ln Likelihood	B$_0$ (±SE)	B$_1$ (±SE)
a) 16 species, >800 m					
Δ minimum elevation (m)	5.71	-0.63**	-89.86	212.2 (±60.1)**	-159.3 (±52.9)**
Δ maximum elevation (m)	9.53	0.89***	-86.12	61.1 (±38.5)^{NS}	299.1 (±41.7)***
Δ LR modelled area ≥10%	4.13	0.81***	13.39	-0.32 (±0.12)*	0.33 (±0.07)***
Δ HOF modelled area ≥10%	4.47	0.85***	13.02	-0.37 (±0.11)**	0.41 (±0.07)***
Δ LR modelled area ≥20%	4.51	0.87***	17.12	-0.34 (±0.09)**	0.35 (±0.05)***
Δ HOF modelled area ≥20%	6.93	0.88***	15.68	-0.32 (±0.08)**	0.41 (±0.06)***
Δ LR modelled area ≥50%	15.50	0.85***	8.10	-0.50 (±0.10)***	0.57 (±0.10)***
Δ HOF modelled area ≥50%	15.50	0.84***	8.85	-0.46 (±0.10)***	0.53 (±0.09)***
b) 15 species, >800 m					
Δ minimum elevation (m)	5.03	-0.62*	-84.41	205.3 (±68.2)*	-197.2 (±69.4)*
Δ maximum elevation (m)	12.10	0.84***	-80.87	71.0 (±39.1)^{NS}	331.6 (±59.4)***
Δ LR modelled area ≥10%	4.39	0.63*	12.16	-0.32 (±0.12)*	0.30 (±0.10)*
Δ HOF modelled area ≥10%	4.83	0.69**	11.92	-0.37 (±0.11)**	0.40 (±0.10)**
Δ LR modelled area ≥20%	4.35	0.78***	15.55	-0.35 (±0.10)**	0.37 (±0.08)***
Δ HOF modelled area ≥20%	7.18	0.76***	14.19	-0.32 (±0.08)**	0.40 (±0.10)**
Δ LR modelled area ≥50%	15.50	0.89***	11.24	-0.48 (±0.08)***	0.87 (±0.12)***
Δ HOF modelled area ≥50%	15.50	0.84***	9.96	-0.44 (±0.09)***	0.75 (±0.13)***
c) 7 species, <800 m					
Δ minimum elevation (m)	4.22	-0.57^{NS}	-37.45	27.2 (±67.3)^{NS}	-174.3 (±113.4)^{NS}
Δ maximum elevation (m)	15.50	0.72^{NS}	-39.93	-65.0 (±91.6)^{NS}	376.5 (±162.8)^{NS}
Δ LR modelled area ≥10%	3.95	0.67^{NS}	11.73	0.06 (±0.05)^{NS}	0.21 (±0.10)^{NS}
Δ HOF modelled area ≥10%	1.87	0.93**	16.08	-0.03 (±0.04)^{NS}	0.30 (±0.05)**
Δ LR modelled area ≥20%	3.64	0.70^{NS}	8.98	0.09 (±0.08)^{NS}	0.33 (±0.15)^{NS}
Δ HOF modelled area ≥20%	4.30	0.86*	10.98	0.01 (±0.06)^{NS}	0.44 (±0.12)*
Δ LR modelled area ≥50%	7.50	0.55^{NS}	1.07	0.17 (±0.23)^{NS}	0.70 (±0.48)^{NS}
Δ HOF modelled area ≥50%	6.50	0.38^{NS}	-0.90	0.35 (±0.31)^{NS}	0.59 (±0.63)^{NS}

a) 16 species not found below 800 m; b) 15 species not found below 800 m, excluding one outlier (*H. lycaon*); c) 7 species found below 800 m.

b) 2005 vs 1967-73

Dependent variable	Alpha†	R	Ln Likelihood	B0 (±SE)	B1 (±SE)
a) 15 species, >800 m					
Δ minimum elevation (m)	15.50	-0.46 ^{NS}	-84.97	195.23±49.99**	-132.26±69.94 ^{NS}
Δ maximum elevation (m)	7.61	0.85***	-83.64	98.99±51.07 ^{NS}	370.3±64.38***
Δ LR modelled area ≥10%	5.70	0.60*	14.36	0.28±0.09**	0.2±0.07*
Δ HOF modelled area ≥10%	7.18	0.61*	11.80	0.34±0.09**	0.24±0.09*
Δ LR modelled area ≥20%	8.24	0.63*	12.96	0.28±0.08**	0.24±0.08*
Δ HOF modelled area ≥20%	9.00	0.65**	13.29	0.27±0.08**	0.24±0.08*
Δ LR modelled area ≥50%	15.50	0.79***	9.02	0.32±0.1**	0.49±0.11***
Δ HOF modelled area ≥50%	15.50	0.59*	2.55	0.15±0.16 ^{NS}	0.44±0.17*
b) 7 species, <800 m					
Δ minimum elevation (m)	3.33	-0.48 ^{NS}	-37.13	42.16±78.58 ^{NS}	-165.41±135.4 ^{NS}
Δ maximum elevation (m)	15.50	0.44 ^{NS}	-40.97	25.89±130.3 ^{NS}	262.01±242.4 ^{NS}
Δ LR modelled area ≥10%	7.18	0.61*	11.80	0.08±0.05 ^{NS}	0.21±0.12 ^{NS}
Δ HOF modelled area ≥10%	15.50	0.55*	11.76	0.02±0.05 ^{NS}	0.2±0.14 ^{NS}
Δ LR modelled area ≥20%	5.21	0.64*	9.75	0.14±0.07 ^{NS}	0.34±0.18 ^{NS}
Δ HOF modelled area ≥20%	9.00	0.65**	13.29	0.07±0.06 ^{NS}	0.43±0.16 ^{NS}
Δ LR modelled area ≥50%	15.50	0.79***	9.02	0.41±0.22 ^{NS}	0.73±0.6 ^{NS}
Δ HOF modelled area ≥50%	15.50	0.52*	-2.48	0.33±0.38 ^{NS}	1.42±1.04 ^{NS}

a) 15 species not found below 800 m (same as 2004 excluding P.apollo) ; b) 7 species found below 800 m. Δ = change in variable, regressed against proportion change in occupancy. †Maximum likelihood estimate of alpha – higher values show lower phylogenetic constraint. Area models: LR – logistic regression (Table S1); HOF – Huisman-Olff-Fresco (Table S2). Significance tested using N-2 degrees of freedom: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ^{NS} $P \geq 0.05$.

Table S4 Tests of models using temperature associations in 1967-1973 to predict high-elevation species distributions in 2004, and vice versa.

a) Predictions of 2004 distributions using 1967-1973 temperature associations

Species	N_P	N_A	-2LL	R^2	Chi^2
Argynnis adippe	29	61	101.33	0.17	11.81**
Argynnis aglaja	27	61	100.33	0.13	8.18**
Argynnis paphia	22	63	88.77	0.14	8.44**
Coenonympha arcania	19	76	92.52	0.04	2.56^{NS}
Erebia meolans	14	79	65.26	0.24	13.54***
Erebia triaria	34	61	84.86	0.46	39.06***
Hesperia comma	49	39	75.59	0.54	45.26***
Hipparchia alcyone	45	42	101.01	0.27	19.49***
Hyponephele lycaon	62	31	107.76	0.15	10.64**
Lycaena alciphron	32	44	73.31	0.44	30.15***
Lycaena virgaureae	43	49	79.92	0.54	47.23***
Melanargia russiae	12	85	63.68	0.17	8.93**
Melitaea cinxia	11	82	61.76	0.12	5.85*
Parnassius Apollo	9	85	53.84	0.12	5.5*
Pyronia tithonus	50	42	71.30	0.61	55.55***
Satyrus actaea	21	68	51.95	0.60	45.30***

Models used to predict distributions from Table S1a, elevation converted to mean annual temperature (ºC). $N_{P/A}$ = N present / absent in 2004; -2LL is -2 log likelihood ratio of logistic regression model for presence / absence in 2004, using temperature associations in 1967-1973. Significance: *** P <0.001;** P < 0.01;* P < 0.05; ^{NS} P > 0.05.

b) Predictions of 1967-1973 distributions using 2004 temperature associations.

Species	N_P	N_A	-2LL	R^2	Chi^2
Argynnis adippe	18	25	52.16	0.18	6.31*
Argynnis aglaja	14	29	41.44	0.36	12.83***
Argynnis paphia	9	33	28.52	0.47	15.13***
Coenonympha arcania	9	31	41.21	0.05	1.24^{NS}
Erebia meolans	7	34	26.65	0.39	10.83**
Erebia triaria	12	26	39.10	0.28	8.3**
Hesperia comma	13	26	38.90	0.33	10.74**
Hipparchia alcyone	8	34	34.43	0.23	6.47*
Hyponephele lycaon	6	34	27.90	0.24	5.92*
Lycaena alciphron	18	22	44.77	0.30	10.28**
Lycaena virgaureae	14	30	44.93	0.29	10.12**
Melanargia russiae	12	32	35.51	0.44	16.05***
Melitaea cinxia	16	21	44.62	0.20	5.99*
Parnassius Apollo	20	24	49.59	0.30	11.05**
Pyronia tithonus	11	27	29.45	0.50	16.28***
Satyrus actaea	18	26	50.09	0.26	9.45**

Models used to predict distributions from Table S1b, elevation converted to mean annual temperature (ºC). $N_{P/A}$ = N present / absent in 1967-1973; -2LL is -2 log likelihood ratio of logistic regression model for presence / absence in 1967-1973, using temperature associations in 2004. Significance:*** P < 0.001;** P < 0.01;* P < 0.05; ^{NS} P > 0.05.

CAPÍTULO II: The contributions of topoclimate and land cover to species distributions and abundance: fine resolution tests for a mountain butterfly fauna.

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Cover photograph: Mating pair of *Hesperia comma* in the transect “La Morcuera”. Photo: Robert J. Wilson

ABSTRACT

Aim Models relating species distributions to climate or habitat are widely used to predict global change effects on biodiversity. Most such approaches assume that climate governs coarse scale species ranges, whereas habitat limits fine scale distributions. We tested the influence of topoclimate and land cover on butterfly distributions and abundance in a mountain range, where climate may vary as markedly at a fine scale as land cover.

Location Sierra de Guadarrama (Spain, southern Europe)

Methods We sampled the butterfly fauna of 180 locations (89 in 2004, 91 in 2005) in a 10800 km^2 region, and derived GLMs for species occurrence and abundance based on topoclimatic (elevation and insolation) or habitat (land cover, geology and hydrology) variables sampled at 100 m resolution using GIS. Models for each year were tested against independent data from the alternate year, using the area under the receiver operating characteristic curve (AUC) (distribution) or Spearman's rank correlation coefficient (r_S) (abundance).

Results In independent model tests, 74% of occurrence models achieved AUCs of >0.7, and 85% of abundance models were significantly related to observed abundance. Topoclimatic models outperformed models based purely on land cover in 72% of occurrence models and 66% of abundance models. Including both types of variables often explained most variation in model calibration, but did not significantly improve model cross-validation relative to topoclimatic models. Hierarchical partitioning analysis confirmed the overriding effect of topoclimatic factors on species distributions, excepting several species for which the importance of land cover was confirmed.

Main conclusions Topoclimatic factors may dominate fine resolution species distributions in mountain ranges where climate conditions vary markedly over short distances and large areas of natural habitat remain. Climate change is likely to be a key driver of species distributions in such systems and could have important effects on biodiversity. However, continued habitat protection may be vital to facilitate range shifts in response to climate change

Keywords Abundance, AUC, distribution maps, elevational range, GIS, GLM, hierarchical partitioning, Iberian Peninsula, Lepidoptera, species range margins.

INTRODUCTION

Models predicting species distributions and abundance are widely used in ecology and biogeography, both to investigate the fundamental determinants of species geographic ranges (e.g., Parmesan *et al.*, 2005; Soberón, 2007) and to predict effects of global change on the conservation of biodiversity (e.g., Thomas *et al.*, 2004; Araújo & Guisan, 2006). Species distribution modelling could play an important role in adapting conservation to climate change, by identifying landscapes in which species are likely to be persistent in the face of change, as well as regions where range shifts can be facilitated by conservation interventions (Hannah *et al.*, 2002). However, two related lines of evidence suggest that pure bioclimate models may be insufficient for many species at the relatively fine scales (local, regional and national) where most conservation planning and management occur. First, it is commonly considered that geographic ranges are limited at a coarse scale by climatic and other abiotic conditions (Huntley *et al.*, 1995; Parmesan *et al.*, 2005), whilst fine-scale species distributions (within climatically-favourable regions) are thought to be more limited by colonization-extinction dynamics and the distributions of suitable habitats and interacting species (Kerr at al., 2001; Luoto *et al.*, 2007; Soberón, 2007). Second, there is strong evidence that species have not extended their ranges to occupy the geographic extent of suitable climates either historically (Araújo & Pearson, 2005), or during recent rapid climate change, because suitable habitats may be too isolated to permit colonizations in highly modified landscapes (White & Kerr 2007; Menéndez *et al.*, 2007). As a result, accurate information on the nature and distribution of habitat and interacting species may be vital, both to model species distributions at a variety of spatial scales, and to assess whether habitat availability is likely to constrain range shifts in response to climate change (Pearson & Dawson, 2003; Hampe, 2004; Pearson *et al.*, 2004; Araújo & Luoto, 2007; Heikkinen *et al.*, 2007; Luoto *et al.*, 2007).

Ecological communities in mountains are often diverse and rich in endemics (e.g. Rahbek & Graves, 2001), but these communities are subject to high expected levels of climate change (Nogués-Bravo *et al.*, 2007). Therefore, determining the consequences of climate change for mountain biodiversity is a priority for conservation biology. Species may track suitable climate conditions more rapidly in mountains than in flat landscapes, for two important reasons: first, climate conditions change markedly with steep elevation gradients, reducing the geographic distances that need to be covered; and second, many mountain regions have been subject to historically low levels of human exploitation and therefore retain relatively large areas of natural habitat (Nogués-Bravo *et al.*, 2008), potentially allowing species to colonize a large proportion of climatically favourable space. The distributions of many species have already shifted uphill in mountains associated with recent warming (e.g., Hill *et al.*, 2002; Konvicka *et al.*, 2003); when lower elevation limits shift uphill, the consequence is usually a reduction in regional distribution sizes (Wilson *et al.*, 2005). In addition, large scale bioclimate models of species distributions sometimes show poor fits to species distributions in mountains (Hill *et al.*, 2002; Trivedi *et al.*, 2008), partly because the fine scale effects of topographic variation on (micro-)climates are masked in coarse scale analyses. There is therefore a great need for fine scale models to predict the effects of climate change and habitat availability on species distributions in mountain ranges.

Here we test the roles of topoclimate and factors which contribute to habitat availability (land cover, geology, river length) for predicting species distributions and abundance in a mountain range that has been subject to recent climate warming. In the Sierra de Guadarrama (central Spain) mean annual temperatures rose by 1.3 ºC between 1967-1973 and 1997-2003 (equivalent to an uphill shift in isotherms of 225 m), whilst mean annual rainfall showed no significant change (Wilson *et al.*, 2005). Over the same time period the lower elevation limits of 16 butterfly species shifted upwards by an average of 212 m, while butterfly communities with comparable species compositions shifted upwards by 293 m (Wilson *et al.*, 2005, 2007). We inferred in these earlier papers (from the patterns observed) that climate was a key driver of butterfly species distributions, and that species had responded to climate change with little time delay. We now test whether current species distributions (in 2004 and 2005) can be modelled accurately at a fine resolution using topoclimatic variables, or whether habitat and land cover factors play an important additional role. We employ detailed fine scale, recent information on land cover, as well as a relatively fine scale (100 x 100 m) Digital Elevation Model. By sampling and modelling butterfly distributions at distinct sites in 2004 and 2005 we are able to carry out robust tests of the ability of the models to predict species occurrence or abundance at independent locations, and of the consistency of topoclimatic or land cover variables selected by the models.

MATERIALS & METHODS

Study system

The study system includes 10800 km^2 of central Spain, with the south-west corner at 40º20'N 4º40'W (UTM reference 30TUK8050) and the north-east corner at 41º28'N 3º36'W (UTM

30TVL7070). This region includes plains with elevations of ≥500 m (in the south) and ≥700 m (in the north), separated by the Sierra de Guadarrama mountain range, with a maximum elevation of 2430 m.a.s.l. (Fig. 1). Dominant vegetation types are evergreen broadleaf woodland (largely *Quercus rotundifolia*) at elevations below 1000 m, deciduous woodland (largely *Quercus pyrenaica*) at roughly 1000-1500 m, and coniferous woodland (*Pinus sylvestris*) at approximately 1500-2000 m. Scrub and open grassland are present at all elevations, including beyond 2000 m. Each of these general vegetation types has a recognisable characteristic associated flora and structure (Rivas-Martínez *et al.*, 1987).

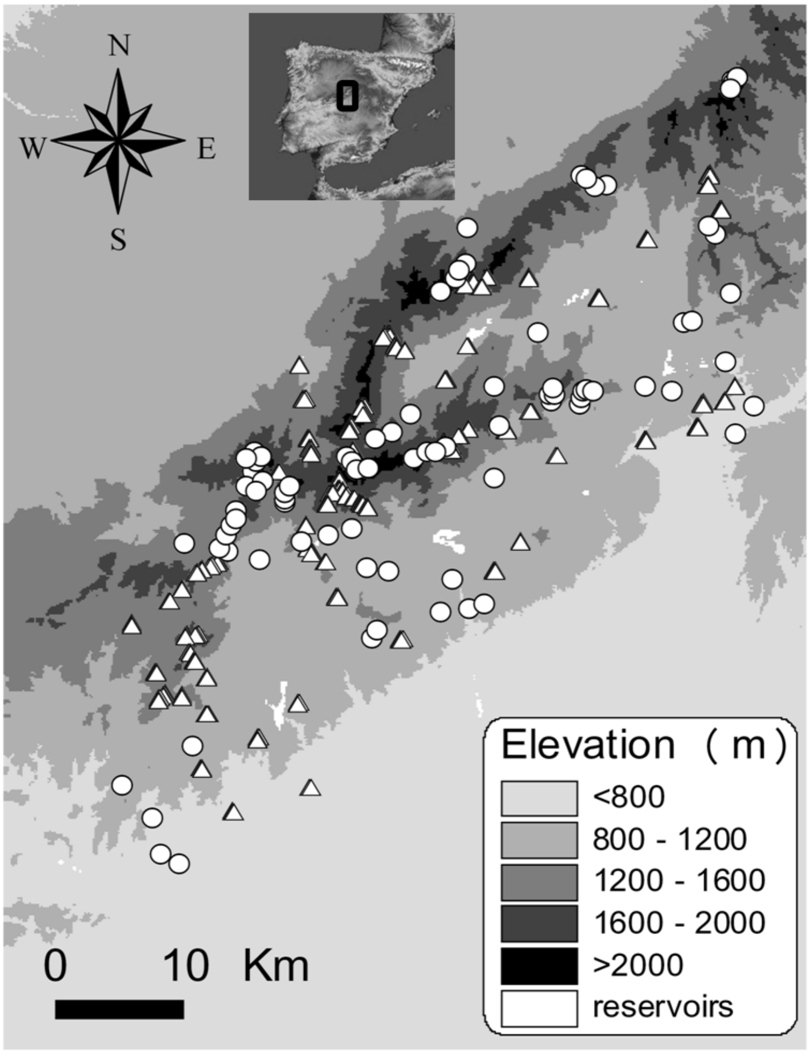


Figure 1 Map of the Sierra de Guadarrama showing elevation and sample sites. Elevation is shown in 400 m bands from <800 m (pale grey) to >2000 m (black). Sample sites are triangles (2004) and circles (2005).

Butterfly data

Survey sites were accessible open areas of natural or semi-natural habitat (usually woodland clearings, scrub or pasture), with comparable numbers of sites in each 200 m elevation band. Butterflies were sampled at 89 sites in 2004 (elevational range 651-2260 m), and 91 spatially-independent sites in 2005 (elevational range 596-2303 m). In both surveys, butterflies were counted on standardized 500 m long x 5 m wide transects during suitable conditions for butterfly activity (Pollard & Yates, 1993).

Ten sites per year were sampled every two weeks between April and October; the remainder of sites were sampled every three weeks, from late May to August 2004 (four times in total) or early May to August 2005 (five times in total). Sites sampled every two weeks were used to estimate weighted mean flight date for each butterfly species. Presence/absence and abundance data for each site were based on four visits: we include the four visits to the two-weekly transects that correspond most closely to the average date of each three-weekly visit; for 2005, we analyse data from the first four visits for spring-flying species (with weighted mean flight date before 1 July 2005) and the second to fifth visits for summer-flying species (with mean flight after 1 July 2005). Species were considered present at sites if at least one individual was observed during the four sample visits (absent if none were counted); abundance was estimated as the sum count from four visits.

In order to ensure that analyses include species whose distributions were representatively sampled, we exclude from analysis (a) species with weighted mean flight dates before May 27th in both years, (b) tree-living species (e.g. *Thecla quercus*) which are likely to be under-recorded by transects, and (c) four genera which were difficult to distinguish in the field (*Carcharodus*, *Mellicta*, *Pyrgus*, *Satyrium*). Species that were present in fewer than 10% or more than 90% of sites are also excluded, since very high or low prevalence (proportion of presences and absences for each species) are likely to reduce discriminatory power between suitable and unsuitable sites.

Spatial autocorrelation can influence the reliability of biogeographic analyses, particularly based on sample sites separated by short geographic distances (Algar *et al.*, 2009). We ensured that survey sites in each elevation band were represented in different parts of the study region, and were selected to be located in separated 1 km grid squares. Mean distance between nearest neighbouring sites was 2.2 km ± SE 0.2 in 2004, and 1.9 km ± SE 0.2 in 2005. In practice, the geographically closest sites (at high elevations, where potential sample sites were limited) were widely separated in elevation; and at lower elevations most sites were much further apart. To detect spatial autocorrelation in our data, we calculated Geary´s *c* coefficient (Geary, 1954; Fortin *et al.*, 1989) for 2004 and 2005 species abundance at each site. Geary´s *c* is recommended instead of Moran´s *I* when the response variable is not normally distributed (Schofield *et al.*, 2007; Maestre *et al.*, 2008), because it takes into account the differences between observed values in two different sites, without using the average value of the response variable (Fortin & Dale, 2005). Only five species in 2004 (*Hipparchia statilinus*, *Lycaena phlaeas*, *Maniola jurtina*, *Melitaea cinxia* and *Pyronia bathseba*) and four in 2005 (*Argynnis paphia*, *Inachis io*, *Maniola jurtina*, *Lampides boeticus*) showed correlograms with any autocorrelated distance classes between sites ($P < 0.01$). Excluding these eight species from analysis did not lead to any differences in the direction or significance of our results (data not shown).

Environmental data

We used 100 x 100 m resolution data, which has been shown effective for butterfly distribution modelling at a regional scale (e.g., Heikkinen *et al.*, 2007). Environmental layers were obtained from three sources: (1) a digital elevation model of the area shown in Fig. 1, which was obtained at 80 x 80 m resolution and interpolated to 100 x 100 m (NASA/JPL-Caltech 2004); (2) regional land cover maps obtained in vector format at 1:50000 scale (CAM, 1998; Ministerio de Medio Ambiente, 2000, 2002a b, 2003), which showed good agreement for all transects with our own field observations of general vegetation type (see below); and (3) a regional geology map also obtained in vector format (SIEMCALSA, 2001). Vector data from the land cover and geology maps (minimum cartographic unit 2.25 ha) was used to determine the proportion contribution of each land cover or geology type to each 100 m grid cell. Universal Transverse Mercator (UTM) coordinates were estimated to the nearest metre at least every 100 m along each transect in the field, using a handheld Garmin GPS unit and recording main vegetation types, which allowed ground-truthing of remotely sensed data. The coordinates were used to plot each transect in ArcGIS 8.1 (ESRI, 2001). Each environmental variable was measured for each transect as the average for 100 m grid squares intercepted by the transect.

Environmental variables were classified as relating either to “topoclimate” or “land cover”. Topoclimatic variables were derived from the 100 m digital elevation model, and included elevation (m), its square term, and estimated solar insolation for the summer and winter solstices (kWh/m^2). Elevation is a complex topographic variable related to climate parameters, including temperature, radiation intensity and rainfall. Annual mean temperature decreases by ca. 5.8-5.9°C, and annual rainfall increases ca. 683-767 mm per 1000 m elevational increase in the study area (relationships with $r^2 > 0.90$ for 1967-1973 and 1997-2003; Wilson *et al*., 2005), suggesting strong thermal and humidity gradients with elevation. These climatic gradients are based on a limited number of meteorological stations (10-11), hence we used elevation and theoretical insolation intensity instead of estimated temperature and rainfall in our models. In comparable studies which were conducted over large areas with limited elevational variation (e.g., Parviainen *et al.* 2008), regional or national climate data interpolated at coarse resolutions were used to model species distributions. However, the Sierra de Guadarrama is a mountain range with a relatively small extension and a marked elevational gradient. The high topographic diversity and limited number of meteorological stations mean that any interpolated climate database may be subject to large errors. Solar insolation parameters were obtained by implementing the *Solar analyst* tool (Fu & Rich, 2000) in ArcView 3.1, which estimates the incoming radiation to a grid cell using the slope, aspect, curvature, elevation and shading effects from surrounding topography. Slope, aspect and curvature were not included as additional topoclimatic variables since their effects are included in the estimates of solar radiation.

Land cover types were first grouped as corresponding to the major classes of evergreen broadleaf forest, deciduous broadleaf forest, coniferous forest, juniper forest, shrubland, meadows/pasture, bare rock, crops, or artificial (human infrastructure, reservoirs etc). In the region these variables correspond well to variation in structural complexity, and in the distribution of grass, herb and shrub species which represent the larval host plants and nectar sources for most species studied (see Rivas-Martínez *et al*., 1987). Classes which were present on fewer than 10% of transects (juniper, bare rock, crops, artificial) were not included as independent variables in the analyses, leaving a final variable list of deciduous forest, coniferous forest, shrubland and meadows/pasture. We calculated a “total forest” variable as the combination of "coniferous" plus "deciduous" plus "evergreen broadleaf" plus "juniper", to account for species broadly associated with tree cover. The land cover map was also used to calculate mean river length (in km) in each 100-m grid cell. River length was included because of its likely effects on humidity, and the distributions and physiological condition of host plants (butterfly species richness has been shown to be greatest in wet habitats elsewhere in Spain; Stefanescu *et al.*, 2004). We grouped geological data into the broad classes of metamorphic rocks (predominantly gneiss), granites, and limestone. Limestone was present on only 8 transects and was not included as an environmental variable. Cover of gneiss and granites were strongly negatively correlated (Spearman's rank correlation coefficient, r_s = -0.932, P <0.001, n = 180), and so only gneiss was included as an environmental variable. Of the final variables selected for analysis, none were highly correlated (absolute r_s values < 0.5) apart from elevation and its square term. The final set of explanatory variables is listed in Table 1.

Table 1 List of environmental variables included in the analyses.

Environmental variable	Code	Mean (min-max)
a) Topoclimatic variables		
Elevation (km)	ELEVN	1.443 (0.596-2.303)
Elevation^2	ELEVN2	
Winter solstice insolation intensity (kWhJ/m^2)	WINTER	0.728 (0.064-1.373)
Summer solstice insolation intensity (kWh/m^2)	SUMMER	5.171 (4.554-5.694)
b) Land cover variables		
Deciduous forest (proportion cover)	DECID	0.106 (0-1)
Shrubland (proportion cover)	SHRUB	0.313 (0-1)
Pasture / meadows (proportion cover)	MEADOW	0.130 (0-1)
Coniferous forest (proportion cover)	PINE	0.277 (0-1)
Total forest (proportion cover)	FOREST	0.462 (0-1)
Metamorphic rock (proportion cover)	GNEISS	0.499 (0-1)
River length (length in km)	RIVER	0.01 (0-0.96)

Model calibration

We generated generalized linear models for the distributions (presence-absence data) and abundance (count data) of those butterfly species satisfying the criteria for analysis. The models for presence-absence data were fitted using a binomial error structure and logit-link function (binary logistic regression) with SPSS software (Norusis, 1998). For the abundance models, the distribution of the response variable is potentially a count from zero to infinity, so we applied a quasi-likelihood estimation of the regression coefficients using a log-link to avoid over dispersion and setting the variance equal to the mean, using S-PLUS software (Venables & Ripley, 1997; MathSoft, 1999). The GLMs were built using forward selection from a null model to select explanatory variables. At each step, one term was added following p-value significance (presence-absence models, $P < 0.05$ for variable inclusion, $P > 0.10$ for removal) or the Mallow's C_p statistic criterion (abundance models), until no additional terms improved the model. Mallow's C_p (StatSci Division, 1996) is an information theory statistic criterion directly derived from AIC, which provides a convenient criterion for determining whether a model is improved by adding or dropping a term (Pennings *et al.*, 2005).

We generated three distribution models and three abundance models for each species in each year. A "Topoclimate" model used stepwise selection from the four topoclimatic variables; the "Habitat" model selected from the seven land cover variables; the "Combined" model selected from all variables (see Table 1 for variable classification).

Model evaluation

Models were evaluated by two methods. The first method (verification) was based on plotting the observed response values (presence-absence or abundance) used for calibration against the values predicted by the model. The second method was a cross-validation test carried out using 2004 models to predict presence-absence or abundance at the independent locations in 2005, and vice versa. For presence-absence models, model evaluation was performed using the area under the receiver operating characteristic curve (AUC), which is independent of species prevalence and decision threshold effects (Pearce & Ferrier, 2000). AUC has been widely used to assess performance of species distribution models (e.g., Luoto *et al.*, 2007; Parviainen *et al.*, 2008; Pöyry *et al.*, 2008; Marmion *et al.*, 2009; Menke *et al.*, 2009) although potential drawbacks to the approach have been identified (see Lobo *et al.*, 2008). We used the non-parametric Mann-Whitney technique to calculate the significance of the AUC because it makes no distribution assumptions. For the abundance models, performance was evaluated using Spearman's r_s, by correlating observed abundance at each site with that predicted by the abundance model from the alternate year (see Thomson *et al.*, 2007).

We tested for differences between overall performances of each model type (AUC for distribution, r_s for abundance), using Wilcoxon's signed-rank tests for dependent samples because different measurements of model performance were calculated for the same species. We also performed additional analyses to test for (1) differences between years (Wilcoxon's signed-rank tests), (2) consistency between species (r_s), and (3) consistency between distribution and abundance (r_s) in model performance.

The six models for each year were used to plot predicted distribution or abundance maps in GIS for the entire study area. For predicted presence-absence maps, raw probability of presence was transformed to Real *et al.*'s (2006) "favourability index", which takes account of species prevalence in the calibration data and therefore controls for changes in prevalence between years (Nielsen *et al.*, 2008).

Hierarchical partitioning

We used hierarchical partitioning (HP) analyses to calculate the independent contribution of each predictor to the distribution or abundance of each butterfly species. In HP, all possible models for the distribution or abundance of each species were considered in a hierarchical multivariate regression setting. HP involves measuring the increase in the goodness-of-fit of all models with a particular variable compared to the equivalent model without that variable (Mac Nally & Horrocks, 2002; Luoto *et al.*, 2006; Radford & Bennett, 2007). The improvement in fit is then averaged across all possible models in which that variable occurs to provide a measure of its independent effects. Thus, for inferring probable causality in multivariate data sets, HP is considered superior to other multiple regression techniques (Watson & Peterson, 1999).

Hierarchical partitioning was conducted using the 'hier.part' package (Mac Nally & Walsh, 2004), implemented in R version 2.1.0 (R Development Core Team, 2005). We specified a logistic model using a multi-trial binomial (occupancy) or Poisson (abundance) distribution with log-likelihood as the goodness-of-fit measure. As a result, HP returned for each species the independent contribution of each explanatory variable. The total independent contribution is not equal to the total explained variance, but is a fraction of the total variance which also includes joint contributions. Then, for each explanatory variable, we counted the number of species for which its independent contribution was ranked first, second and so on (Radford &

Bennett, 2007), and thereby calculated the average ranked contribution of each variable to butterfly distributions and abundance in the region.

RESULTS

Forty-eight species satisfied the criteria for analysis (Table 2). The relative prevalence of the selected 48 species was correlated between 2004 and 2005 ($r_s = 0.73$, $P < 0.001$, $n = 48$).

Table 2 The species selected for analysis, and the model types which achieved the highest cross-validation scores. Model classification: H – habitat variables; T – topoclimatic variables; C – combined variables. Distribution models are based on presence-absence data and abundance models on count data for the year shown – superscript numbers show AUC (distribution models) or r_s (abundance models) for cross-validation. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant. Species are listed in descending order of total presences in both surveys. $n = 89$ sample sites in 2004, $n = 91$ in 2005. *na* show cases where no variables were significant in model calibration. Nomenclature follows García-Barros *et al.* (2004).

			Distribution models AUC		Abundance models Spearman's r_s	
Species	N pres 2004	N pres 2005	2004	2005	2004	2005
Lycaena paleas	78	68	H$^{0.536\text{ n.s.}}$	C$^{0.528\text{ n.s.}}$	T$^{0.311**}$	H$^{0.214*}$
Melanargia lachesis	68	73	T$^{0.908***}$	T$^{0.918***}$	C$^{0.685***}$	C$^{0.662***}$
Argynnis Pandora	74	63	T$^{0.705**}$	T$^{0.795***}$	H$^{0.222*}$	T$^{0.150\text{ n.s.}}$
Kanetisa circe	58	55	C$^{0.821***}$	C$^{0.852***}$	C$^{0.668***}$	T$^{0.694***}$
Hyponephele lycaon	58	55	T$^{0.936***}$	C$^{0.944***}$	T$^{0.817***}$	C$^{0.560***}$
Lasiommata megera	53	59	T$^{0.701**}$	T$^{0.610\text{ n.s.}}$	H$^{0.170\text{ n.s.}}$	H$^{0.249*}$
Aricia cremera	68	43	T$^{0.766***}$	T$^{0.783***}$	T$^{0.573***}$	T$^{0.675***}$
Argynnis niobe	53	56	T$^{0.770***}$	T$^{0.747***}$	H$^{0.023\text{ n.s.}}$	T$^{0.385***}$
Maniola Justina	61	44	T$^{0.885***}$	T$^{0.877***}$	T$^{0.698***}$	T$^{0.736***}$
Pieris rapae	65	32	na	H$^{0.649\ *}$	T$^{0.230*}$	H$^{0.391***}$
Hipparchia statilinus	48	49	T$^{0.829***}$	C$^{0.826***}$	C$^{0.698***}$	C$^{0.498***}$
Hesperia comma	50	44	T$^{0.817***}$	T$^{0.791***}$	T$^{0.506***}$	C$^{0.664***}$
Pyronia tithonus	49	43	C$^{0.843***}$	T$^{0.930***}$	T$^{0.589***}$	T$^{0.753***}$
Lycaena alciphron	43	49	T$^{0.801***}$	T$^{0.800***}$	T$^{0.537***}$	T$^{0.523***}$

Thymelicus sylvestris	50	41	C$^{0.830***}$	T$^{0.883***}$	T$^{0.526***}$	C$^{0.693***}$
Hipparchia semele	54	35	H$^{0.617\ n.s.}$	H$^{0.516\ n.s.}$	T$^{0.189\ n.s.}$	C$^{0.351**}$
Aglais urticae	44	44	T$^{0.888***}$	T$^{0.921***}$	T$^{0.814***}$	C$^{0.812***}$
Cynthia cardui	76	9	T$^{0.679\ *}$	T$^{0.784**}$	T$^{0.356**}$	T$^{0.446***}$
Aporia crataegi	38	47	T$^{0.753***}$	T$^{0.779***}$	C$^{0.574***}$	T$^{0.647***}$
Hipparchia alcyone	44	37	H$^{0.875***}$	C$^{0.889***}$	C$^{0.641***}$	H$^{0.641***}$
Coenonympha pamphilus	41	40	T$^{0.864***}$	T$^{0.922***}$	C$^{0.709***}$	T$^{0.782***}$
Gonepteryx rhamni	39	42	T$^{0.663**}$	T$^{0.734***}$	H$^{0.363***}$	T$^{0.134\ n.s.}$
Lycaena virgaureae	40	38	T$^{0.919***}$	T$^{0.891***}$	T$^{0.707***}$	C$^{0.750***}$
Argynnis aglaja	28	39	T$^{0.765***}$	H$^{0.749***}$	H$^{0.305**}$	C$^{0.430***}$
Pontia daplidice	26	40	C$^{0.660**}$	H$^{0.611\ n.s.}$	H$^{0.072\ n.s.}$	T$^{0.130\ n.s.}$
Argynnis adippe	29	35	T$^{0.758***}$	H$^{0.825***}$	T$^{0.420***}$	H$^{0.447***}$
Erebia triaria	26	36	T$^{0.854***}$	T$^{0.788***}$	C$^{0.609***}$	C$^{0.471***}$
Argynnis paphia	26	33	H$^{0.877***}$	H$^{0.786***}$	H$^{0.593***}$	H$^{0.450***}$
Polyommatus icarus	37	17	T$^{0.630\ n.s.}$	na	C$^{0.222*}$	C$^{0.480***}$
Lampides boeticus	32	21	na	na	H$^{0.001\ n.s.}$	Na
Inachis io	22	27	C$^{0.701**}$	H$^{0.642\ *}$	H$^{0.222*}$	H$^{0.280**}$
Pyronia bathseba	22	27	T$^{0.822***}$	C$^{0.832***}$	T$^{0.626***}$	C$^{0.540***}$
Lycaena tityrus	28	18	H$^{0.841***}$	T$^{0.883***}$	T$^{0.541***}$	T$^{0.634***}$
Satyrus actaza	24	22	C$^{0.914***}$	C$^{0.910***}$	C$^{0.584***}$	C$^{0.647***}$
Pyronia cecilia	21	23	T$^{0.898***}$	T$^{0.926***}$	T$^{0.613***}$	T$^{0.638***}$
Coenonympha arcania	19	20	H$^{0.762***}$	T$^{0.782***}$	H$^{0.209*}$	H$^{0.422***}$
Melitaea Phoebe	16	23	T$^{0.784***}$	T$^{0.775**}$	T$^{0.515***}$	T$^{0.459***}$
Erebia meolans	14	25	C$^{0.892***}$	C$^{0.836***}$	C$^{0.580***}$	C$^{0.464***}$
Melitaea didyma	21	15	H$^{0.538\ n.s.}$	C$^{0.651\ *}$	H$^{0.174\ n.s.}$	C$^{0.219*}$
Lasiommata maera	11	22	T$^{0.765***}$	T$^{0.782**}$	T$^{0.372***}$	H$^{0.367***}$
Iphiclides podalirius	10	22	T$^{0.611\ n.s.}$	T$^{0.714\ *}$	T$^{0.154\ n.s.}$	T$^{0.111\ n.s.}$
Melanargia russiae	14	13	T$^{0.650\ n.s.}$	H$^{0.690*}$	T$^{0.231*}$	C$^{0.358**}$
Glaucopsyche alexis	14	10	C$^{0.781***}$	T$^{0.807***}$	C$^{0.193\ n.s.}$	T$^{0.336**}$
Vanessa atalanta	11	11	na	T$^{0.641\ n.s.}$	H$^{0.307**}$	C$^{0.197\ n.s.}$
Euphydryas aurinia	12	9	H$^{0.862***}$	T$^{0.833***}$	C$^{0.456***}$	C$^{0.331**}$
Pararge Megeria	12	9	H$^{0.873***}$	T$^{0.799**}$	H$^{0.393***}$	C$^{0.393***}$
Melitaea cinxia	13	7	T$^{0.739**}$	T$^{0.785**}$	T$^{0.298**}$	T$^{0.379***}$
Papilio Machain	10	10	na	na	C$^{0.059\ n.s.}$	C$^{0.200\ n.s.}$

Model calibration

Models containing significant effects of at least one environmental variable were obtained for 89 out of 96 potential cases for distribution (48 species in two years), and for 95 out of 96 cases for abundance (Table 2). For combined models, the mean number of variables selected was 2.1 (±SE 0.19) for distribution models, and 4.1 (±SE 0.26) for abundance models. In general, combined and topoclimatic models obtained higher cross-validation scores than purely habitat-based models (details below).

The percentage of models containing each variable is listed in Table 3. Overall, the ranking of variables selected in combined models was consistent between years, for distribution models ($r_s = 0.71$, $P = 0.015$, $n = 11$) and abundance models ($r_s = 0.71$, $P = 0.015$, $n = 11$). Elevation was the most selected variable in topoclimatic and combined models, with a significant unimodal response (i.e., both a positive effect of elevation and a negative effect of elevation^2) in 54% of distribution models and 58% of abundance models. Of the land cover variables, coniferous forest was selected most frequently, but most variables were selected by 10-30% of combined distribution models, and by 20-50% of combined abundance models (Table 3).

Table 3 The percentage of models of each type in which each variable was selected. Top: topoclimatic; Hab: Habitat; Comb: combined. Variable codes as in Table 1.

	% models (48 species)											
	Distribution 2004			**Distribution 2005**			**Abundance 2004**			**Abundance 2005**		
Variables	Top	Hab	Comb	Top	Hab	Comb	Topo	Hab	Comb	Topo	Hab	Comb
ELEVN	77		56	77		52	65		58	63		67
ELEVN2	67		40	69		54	67		63	63		67
WINTER	4		4	8		10	19		25	33		40
SUMMER	13		8	2		2	27		31	33		25
FOREST		25	13		21	15		40	25		29	19
DECID		19	13		25	13		35	29		50	40
SHRUB		25	13		15	4		40	42		40	19
MEADOW		25	4		4	15		35	25		27	15
PINE		56	29		35	21		63	48		56	46
GNEISS		25	13		38	19		48	33		52	44
RIVER		8	10		21	17		27	25		52	38

Model evaluation

Model performance was evaluated using AUC for distribution data (Fig. 2) or r_s for abundance data (Fig. 3). We tested whether model performance was consistent between years, species and type of model (topoclimatic, habitat and combined).

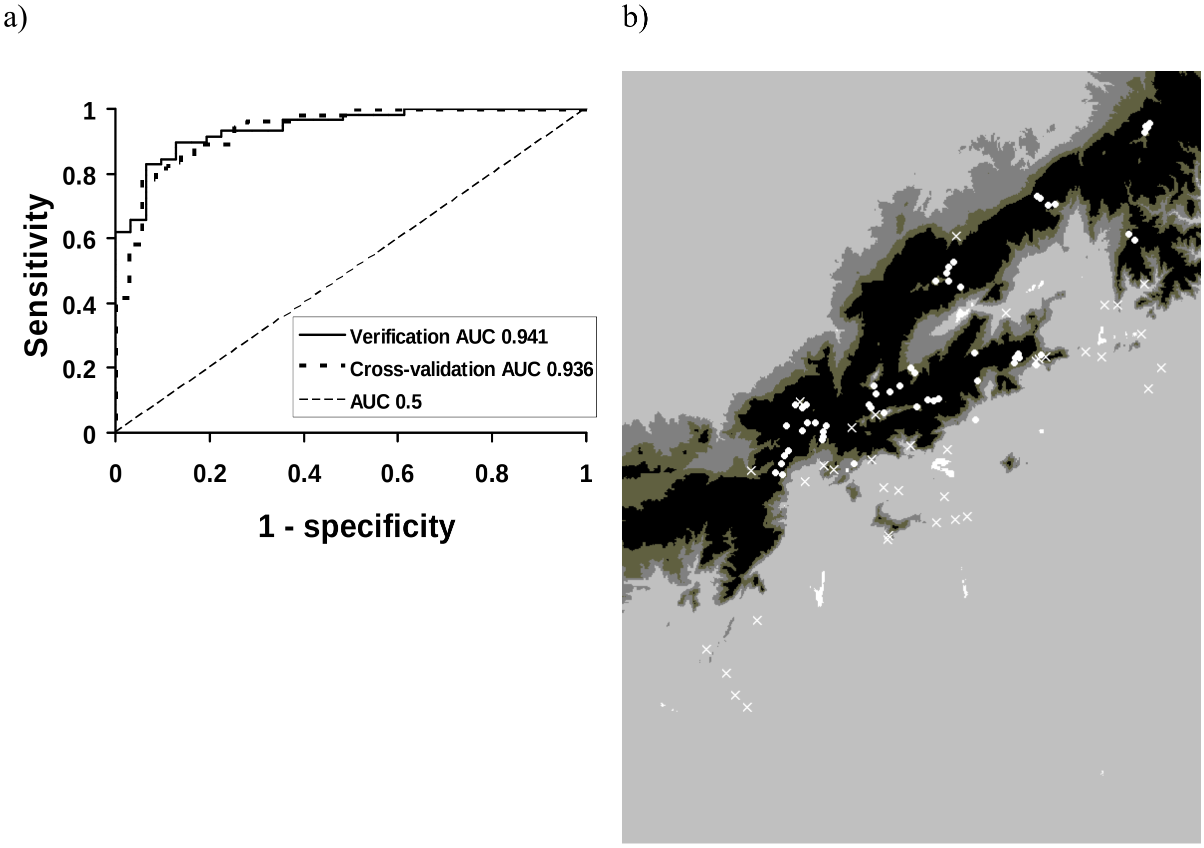


Figure 2 Evaluation and mapping of distribution model for *Hyponephele lycaon*, using 2004 models and topoclimatic variables. Model evaluation (a) is shown as AUC for verification (solid line) and cross-validation years (thick dashed line). AUC = 0.5 is shown as a thin dashed line. The modelled distribution map (b) show “favourability index” (see methods) in 0.25 intervals from pale grey (0-0.25) to black (0.75-1). Observed presence (circles) and absence (crosses) are shown for the cross-validation year (2005). Study area and regional context identical to Fig. 1. Reservoirs shown in white.

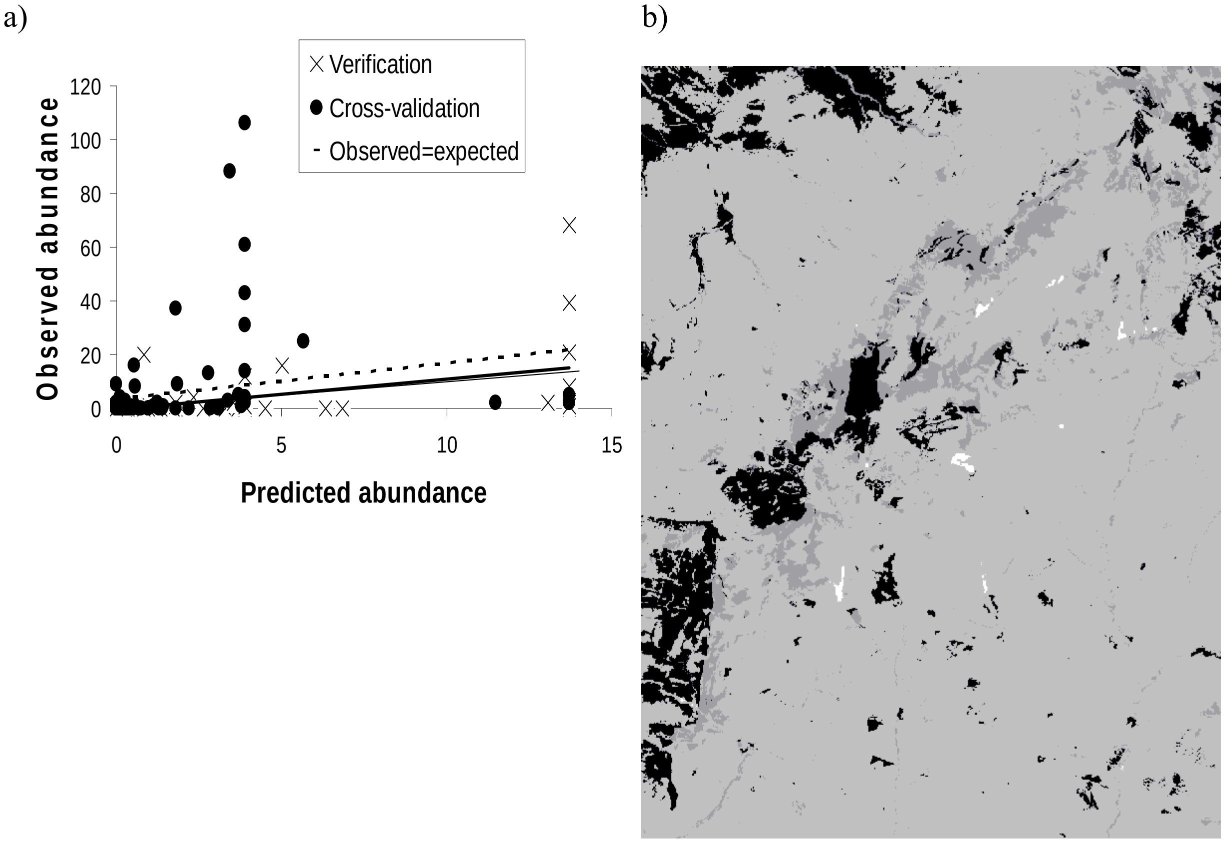


Figure 3 Evaluation and mapping of abundance model for *Argynnis paphia*, using 2004 models and habitat variables. Model evaluation (a) is shown as observed against predicted abundance for verification (crosses; solid regression line) and cross-validation years (circles; thick dashed regression line). Observed = expected is shown as a thin line. The modelled abundance map (b) show predicted abundance of these species from pale grey (0-1 individuals) to black (>10 individuals). Study area and regional context identical to Fig. 1. Reservoirs shown in white.

In model verification, AUC values ranged from 0.61 to 0.99 (total mean 0.78), and r_s from 0.01 to 0.83 (total mean 0.48). There were no differences between years in the performance of distribution and abundance models (all six Wilcoxon's signed-rank tests, $P > 0.1$, $n = 48$). Relative model performance among species was consistent between years (all six correlations, $r_s > 0.5$, $P < 0.001$, $n = 48$), i.e. the species with better performances for a given model type in 2004 were also those with better performances for that model type in 2005. Considering the verification scores for model type, combined models performed better than topoclimatic models, which in turn performed better than habitat models, both for distribution and abundance (all Wilcoxon's signed-rank tests, $P < 0.05$, $n = 48$) (Fig. 4).

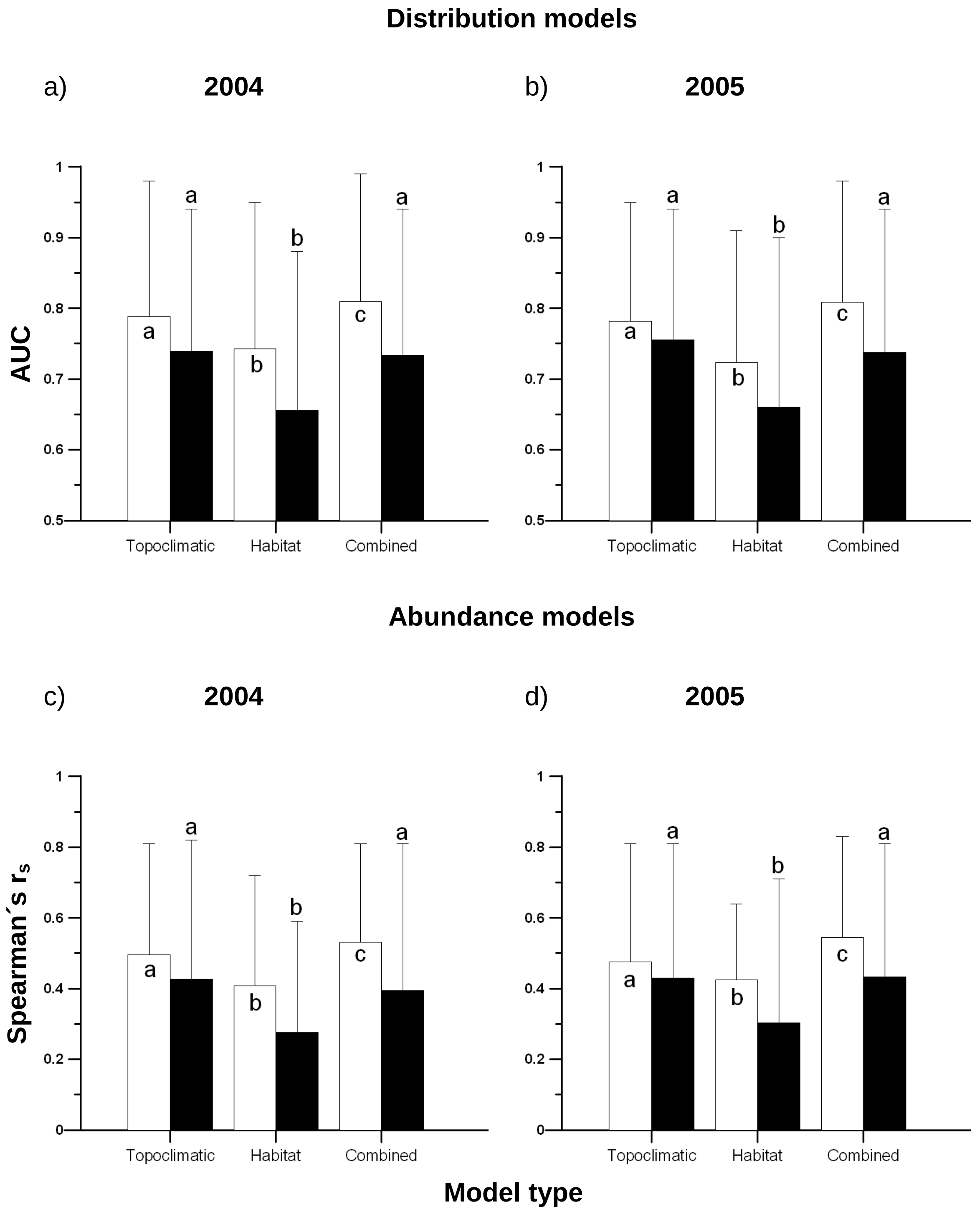


Figure 4 Summary of model evaluation for species distribution (a, b) and abundance (c, d). Models were calibrated using data from 2004 (a, c) or 2005 (b, d) and evaluated using AUC for occurrence models (a, b) and r_s for abundance models (c, d). Bars show mean and maximum values for verification (white) and cross-validation data (black). Different letters show significant differences in performance (AUC or r_s) between model types at $P < 0.05$ (Wilcoxon's signed-rank tests) with independent tests for verification (letters within bars) and cross-validation (letters above bars).

In distribution model cross-validation, AUC values ranged from 0.54 to 0.94 (total mean 0.72). 75% of topoclimatic models, 40% of habitat models and 65% of combined models achieved AUC values above 0.7, indicating good or excellent model performance. For abundance models, r_s values ranged from 0.01 to 0.82 (total mean 0.37). Similarly to model verification, there were no significant differences between years in the performance of distribution or abundance models (all six Wilcoxon´s signed-rank tests, $P > 0.07$, $n = 48$). There was also consistency in the ranking of species for the performance of both distribution and abundance models (all six correlations, $r_s > 0.5$, $P < 0.001$, $n = 48$). Models for distribution or abundance based on topoclimatic or combined variables had significantly higher cross-validation scores than habitat-based models, for both 2004 and 2005 (all eight Wilcoxon's signed-rank tests, $P < 0.001$, $n = 48$) (Fig. 4). There were no significant differences in cross-validation scores between topoclimatic and combined models (all four signed-rank tests, $P > 0.3$, $n = 48$).

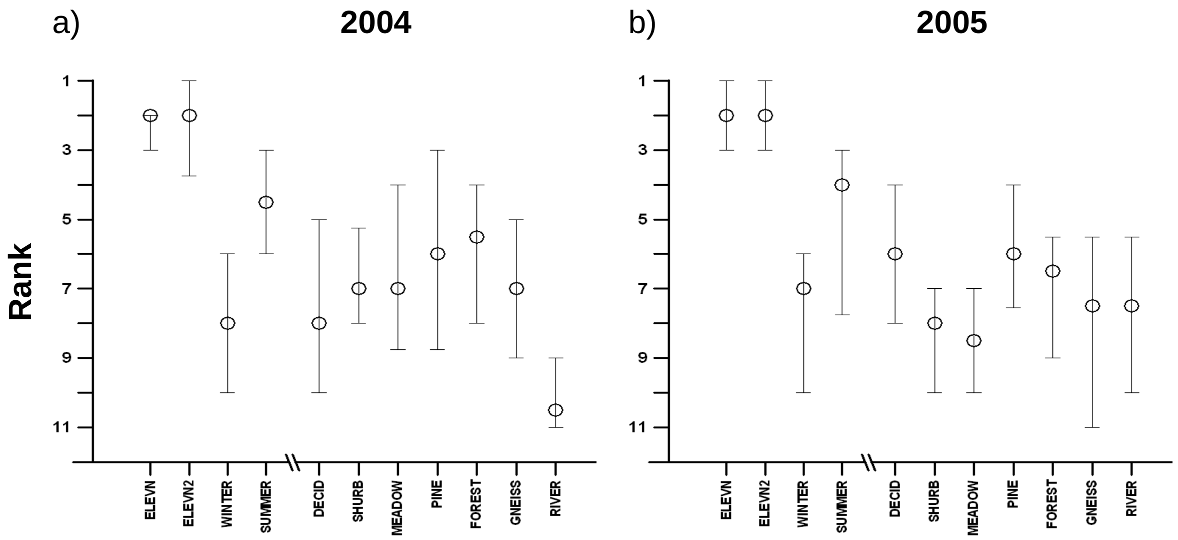
Finally, relative model performance was consistent across species between distribution and abundance models, both using verification (correlation between AUC and r_s, all $r_s > 0.7$, $P < 0.001$, $n = 48$) and cross-validation data (all $r_s > 0.6$, $P < 0.001$, $n = 48$). This consistence between the two approaches leads us to believe that each approach has been generally reliable in this instance.

Although topoclimatic models outperformed habitat models in cross-validation tests in a high proportion of cases for distribution (72%) and abundance (66%), habitat models consistently gave the highest cross-validation scores for some species, for example *Argynnis paphia* (Table 2; Fig. 3).

Hierarchical partitioning

Across all species, elevation returned the highest mean independent contribution in HP, followed by summer solstice insolation intensity, coniferous forest, and total forest (Fig. 5).

Distribution models



Abundance models

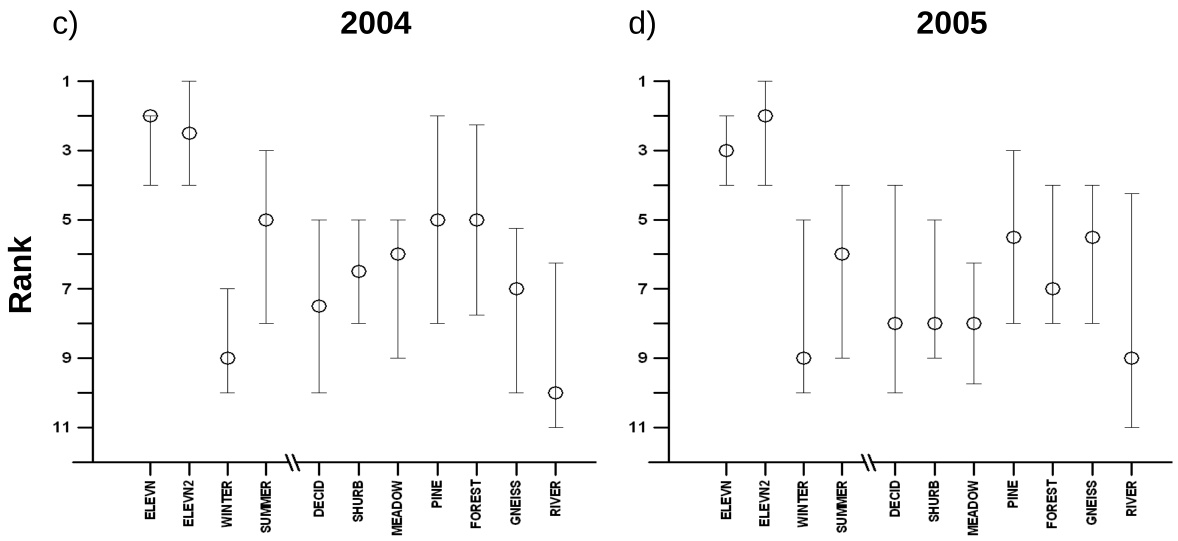


Figure 5 Ranked comparison of the independent contributions of topoclimatic and habitat variables for distribution (a, b) and abundance (c, d) models using data from 2004 and 2005 (n = 48 species). Values represent the median rank (first to eleventh) of each variable in HP analyses based on the magnitude of their independent contribution. Error bars represent the interquartile range. Acronyms used are defined in Table 1.

When species were considered separately, all variables were ranked first for at least one species, except shrubland in distribution models and pasture/meadows in abundance models (Appendix S1). Out of the 48 species considered, elevation or its square term was ranked first for 28 (2004) and 32 species (2005) in distribution models, and for 21 (2004) and 26 species (2005) in abundance models. Among the land cover variables, coniferous forest was ranked first for 11 (2004) and 4 species (2005) in distribution models, and for 10 (2004) and 7 species (2005) in abundance models (Fig. 5). Overall, topoclimatic variables were ranked first for 31 (2004) and 33 species (2005) in distribution models, and for 24 (2004) and 29 species (2005) in abundance models (Appendix S1).

DISCUSSION

In the present study, we examined the contributions of topoclimate and land cover to fine resolution (100 m) butterfly distributions and abundance in a mountain area. Our analyses revealed high concordance in variable selection between models calibrated using different data sources (year 2004 vs. 2005), different response variables (presence-absence vs. abundance) and statistical approaches (GLM vs. HP), supporting the consistency of our results. Concordance between standard modelling (GAM) and partitioning methods (HP) was found in another similar study (Luoto *et al.*, 2006). However, to our knowledge, this is the first study showing consistency between the results for models using data from different years or considering different response variables (distribution vs. abundance): this is probably because most studies are based on presence data from atlas or similar sources combining data from several years, which are only suitable for generating distribution models. It is worth noting that the 2004 and 2005 survey periods were extremely climatically different, with the

2005 summer much hotter and drier than 2004. The summer of 2005 was the driest since 1947 (37% lower precipitation than the annual summer average) and the hottest in the last 15 years in the Iberian Peninsula (1.3ºC hotter than annual average since 1960), whilst 2004 was around 10% cooler and more humid than the summer mean in central Spain (AEMet, 2009). Nevertheless, we found very similar results in both years.

Topoclimatic versus land cover variables

A hierarchical scheme in terms of scale (extent and resolution) has been suggested for the environmental control of species distributions, in which topoclimatic variables are large scale determinants, whilst at regional scales factors including land cover and geology become increasingly important (e.g. Soberón, 2007). At finer scales, factors including biotic interactions and microclimate may be most significant (Pearson & Dawson, 2003). Thus, studies carried out at continental and national extents using relatively coarse resolutions (usually 10-80 km) have shown that species distributions are governed principally by climatic factors (Thuiller *et al.*, 2004; Luoto *et al.*, 2006, 2007). In contrast, land cover variables increase in importance in those studies limited to a smaller extent (regions) and using finer resolution data (100-500 m) (Seoane *et al.*, 2004; Parviainen *et al.*, 2008). Considering the regional extent (10800 km^2), and rather fine resolution (100 m) of our study, we might expect a dominant role of land cover factors in our models. In addition, given that butterfly larvae are phytophagous and frequently feed on a limited range of plant species (associated with particular habitats), relationships of species distributions and abundance with land cover should be stronger than with topoclimate. However, topoclimatic variables entered more frequently and accounted for more independent variance in the models than land cover variables, even though there were fewer topoclimatic variables (4) than land cover variables (7). It is important to highlight here that there were no strong correlations between topoclimatic and land cover variables, suggesting that habitat factors do not represent redundant information for model calibration (c.f. Thuiller *et al*., 2004). This apparent importance of topoclimate accords with evidence that butterfly distribution and diversity patterns in the region have changed markedly in response to recent climate change (Wilson *et al*., 2005, 2007).

At least four, non-exclusive, hypotheses could explain the greater contribution of topoclimate than land cover to species distributions and abundance in this study. First, although our study area has been exposed to a strong urbanisation pressure over recent decades, large areas of natural habitat still remain (land cover is only 11.5% urban and 36.7% intensive agriculture in the whole area). In this sense, mountain areas like the Sierra de Guadarrama are likely to differ from the more heavily modified lowland landscapes where previous distribution modelling exercises contrasting topoclimate and land cover have taken place (e.g., Pearson *et al*., 2004 for Britain). Nevertheless, studies conducted in boreal areas where natural habitats still cover a large proportion of the landscape have found stronger effects of land cover at fine scales (e.g., Luoto *et al*., 2006, 2007; Parviainen *et al*., 2008). Second, mountain areas have a more complex topography than lowland landscapes, consisting of a wide range of elevations and aspects which cause climate conditions to vary markedly over short distances. Third, some species can have apparently ubiquitous and abundant host plants in the study area. This is the case, for instance, of some Lycaenidae (e.g. *L. alchipron* and *L. virgaureae*), which had excellent topoclimatic distribution models (Table 2). Both species were absent from the lowest elevations, whereas their main host plant, *Rumex acetosella*, occurs nearly everywhere in the whole elevational range (95% of sites, $n = 40$, unpublished data). Four, land cover categories could be too coarse to identify close associations with butterflies, whose habitat selection mechanisms may operate at much finer scales (Vane-Wright & Ackery, 1989). Fine-scale topographic and vegetation heterogeneity may play vital roles in determining whether broadly defined land covers such as grassland really represent habitat for species (e.g., Weiss *et al*., 1988; Kerr *et al*., 2001). Hence an explicit resource-based approach to the definition and modelling of habitats for species is likely to be more accurate than procedures based on land cover classes (Vanreusel & Van Dyck, 2007) but at regional scales for relatively poorly documented locations and taxonomic groups, land cover data may represent the only readily available information for modelling species distributions and identifying the general habitat types on which they depend. This study strongly suggests that relatively fine-scale topographic variation, for which data are now widely available, makes an important contribution to probability of occupancy which should not be ignored.

Determinants of species distributions and abundance

Elevation and its quadratic term were the most selected variables, and ranked most highly in variance explained in the distribution and abundance models. Given the apparent importance of topoclimatic variables, there is a need either for fine-scale climate monitoring, or improved techniques for estimating topographic effects on microclimate (e.g., Bennie *et al*., 2008) to generate sound interpolated databases for species distribution models.

It is worth noting that the dominant contribution and higher predictive ability of topoclimatic variables for most species do not imply that climate directly governs species distributions and abundance in all cases. Apart from the issues related to the complex nature of topoclimatic variables such as elevation discussed above, we should take into account that the effects of topoclimate on species distributions and abundance can be both direct and indirect. Direct effects may include the influence on the energetics (e.g., thermoregulation) and physiological tolerance of an organism, whereas indirect effects may include the influence on food availability, presence of competitors, predators or organisms that provide habitat for a species. A good example in the study area is *Aporia crataegi*. Topoclimatic models had the highest predictive ability for distributions in 2004 and 2005, and for abundance in 2005, suggesting a dominant role of topoclimate for this species (Table 2). A detailed study conducted in the Sierra de Guadarrama showed that climatic limitation was the most likely cause for its low elevation range margin, whereas the absence of host plants (*Crataegus monogyna* and *Prunus spinosa*) from high elevations set the upper limit, suggesting a combination of direct and indirect effects to explain its elevational range (Merrill *et al*., 2008). In this case, the host plants (particularly *C. monogyna*) are widespread shrubs that occur in a wide range of habitats from the lowest sites (at ca. 500 m) to ca. 1800 m (unpublished data), which could partly explain the low contribution of land cover variables to models for *A. crataegi*.

Although data on the determinants of elevational range limits are limited for other species in the area, it is encouraging that some of the few species with consistently powerful models based on habitat rather than topoclimate showed results concordant with their biology. The most representative example is *Argynnis paphia*, the only species for which habitat models (including in all cases the variables total woodland and coniferous forest) had the highest performance for distribution and abundance in both years (Table 2). Despite using herbaceous larval host plants (*Viola* spp.), this species is known to lay eggs singly on the bark of tree trunks (Wiklund, 1984), which could explain its association with forested habitats.

Implications for species responses to global change

In two previous studies, we showed that the lower elevation limits of 16 mountain butterfly species, and overall butterfly community composition, respectively increased by 212 m and 293 m from 1967-73 to 2004-05, accompanying a 225 m rise in isotherms (equivalent to 1.3°C) (Wilson *et al*., 2005, 2007). In those papers, we inferred that the elevational range shifts were likely to be driven by climate rather than habitat change, but no explicit tests for relationships between butterfly distributions and land cover were undertaken. The results from this study suggest a dominant role of topoclimate over land cover in explaining butterfly distributions in the Sierra de Guadarrama, providing additional support for the hypothesis of climate-driven distribution changes over the ca. 35-year period. Stefanescu *et al*. (2004) found that topoclimatic factors were the major determinants of species richness in northeast Spain, whereas vegetation variables had an almost negligible effect. In the latter region, climate warming has also been recognised as one of the driving forces of change in butterfly communities (Stefanescu *et al*., 2003).

We were able to produce significant models explaining distribution and abundance for a large proportion (>90%) of the butterflies in the Sierra de Guadarrama. Non-significant models were usually associated with migratory species (*Cynthia cardui*, *Lampides boeticus*, *Pieris rapae*, *Pontia daplidice*, *Vanessa atalanta*, Table 2) whose distributions and abundance probably depend more on large-scale movements of individuals than on local habitat characteristics (e.g., Stefanescu, 2001). In addition, 75% of topoclimatic models achieved cross-validation AUC values above 0.7 (compared to 40% of habitat and 65% of combined models), indicating a good or excellent predictive performance based on topoclimatic variables only. This suggests that models for the climatic associations of a substantial proportion of the butterfly fauna might reasonably indicate the relative regional vulnerability of different species to climate change, the importance of particular sites for conserving these species, and the sensitivity of such conclusions to different climate scenarios. Bioclimate models are now widely used to project distribution change for a wide range of taxa and regions, including butterflies (e.g., Pearson *et al.*, 2004; Luoto *et al.*, 2007; Thomson *et al.*, 2007; Trivedi *et al.*, 2008). Our study provides support for topoclimate-driven species distributions and abundance even at relatively fine scales, but with the proviso that many species may be influenced by additional factors.

Bioclimate models may be of limited value if the main influences of climate on species distributions are through indirect effects via interacting species. Taking the example of *Aporia crataegi*, any elevational expansion projected by topoclimatic models would require host plants to expand at least at the same rate and direction as *A. crataegi*, which is unlikely. It is therefore questionable whether forecasts of species range shifts should be made without taking into account biotic interactions (Araújo & Luoto, 2007). Further studies at different spatial scales concerning the contributions not only of topoclimate and land cover to species distributions and abundance, but also of relevant biotic interactions, are needed to assess the validity of projections from habitat models (e.g. Heikkinen *et al.*, 2007; Bradley & Fleishman, 2008).

CONCLUSIONS

In this study, topoclimatic factors dominated species distributions and abundance in a mountain region, probably because climate conditions vary markedly over relatively short distances and relatively large areas of natural habitat still remain. Thus, in contrast to previous research, the results suggest that topoclimatic models could be an appropriate tool for predicting range shifts based on climate change scenarios at fine resolutions and regional scales, at least in mountainous landscapes. Nevertheless, continued habitat protection may be essential to facilitate range shifts, and evaluation of the role of additional variables influencing biotic interactions may be crucial to assess the applicability of such models.

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SUPPLEMENTARY MATERIAL

Additional supporting information may be found in the online version of this article:

Appendix S1 Ranked comparison of the independent contributions of topoclimatic and habitat variables to explaining the distribution (S1a) and abundance (S1b) of butterfly species. Values represent the number of species (out of 48) for which the rank position of each variable is first to eleventh, based on the magnitude of their independent contribution from hierarchical partitioning analyses. Variable codes as in Table 1.

S1a	Topoclimatic								Habitat													
	ELEVN		ELEVN2		WINTER		SUMMER		DECID		SHRUB		MEADOW		PINE		FOREST		GNEISS		RIVER	
Rank	04	05	04	05	04	05	04	05	04	05	04	05	04	05	04	05	04	05	04	05	04	05
First	8	13	20	19	2	0	1	1	0	3	0	0	3	0	11	4	2	4	1	2	0	2
Second	26	19	9	13	1	4	3	2	2	0	0	1	1	0	0	5	3	3	2	0	1	1
Third	7	11	7	7	1	0	11	12	4	6	2	3	5	3	2	3	4	1	4	2	1	0
Fourth	2	2	5	4	2	4	9	11	1	6	6	1	4	2	5	7	7	2	3	6	4	3
Fifth	3	0	1	3	4	3	6	4	8	8	4	5	3	4	4	4	8	5	7	5	0	7
Sixth	1	0	4	0	4	10	9	2	5	3	10	1	7	5	4	6	2	9	2	7	0	5
Seventh	1	2	2	0	5	5	2	4	3	3	7	9	7	7	4	6	7	4	8	2	2	6
Eighth	0	1	0	0	8	2	0	5	2	8	11	5	6	3	6	8	5	6	7	4	3	6
Ninth	0	0	0	2	6	6	3	1	8	4	3	8	5	11	8	3	6	6	5	3	4	4
Tenth	0	0	0	0	8	7	3	6	9	3	5	10	3	6	4	2	4	7	3	2	9	5
Eleventh	0	0	0	0	7	7	1	0	6	4	0	5	4	7	0	0	0	1	6	15	24	9

S1b	Topoclimatic								Habitat													
	ELEVN		ELVN2		WINTER		SUMMER		DECID		SHRUB		MEADOW		PINE		FOREST		GNEISS		RIVER	
Rank	04	05	04	05	04	05	04	05	04	05	04	05	04	05	05	04	05	04	04	05	04	05
First	2	7	19	19	0	2	3	1	1	2	2	1	0	0	10	7	5	2	5	3	1	4
Second	24	15	5	8	1	2	2	4	2	5	2	1	1	1	3	4	7	4	1	2	0	2
Third	7	12	9	4	2	5	10	4	3	4	2	5	5	1	4	4	3	3	2	2	1	4
Fourth	6	4	4	6	1	1	7	6	3	2	4	3	4	3	6	6	7	4	1	11	5	2
Fifth	3	3	6	4	1	3	4	6	4	6	7	3	6	1	3	3	7	7	3	6	4	6
Sixth	2	4	3	3	4	4	2	7	2	2	7	4	9	6	5	7	4	3	9	6	1	2
Seventh	3	2	0	2	8	2	6	4	9	1	7	6	2	10	2	3	3	12	5	4	3	2
Eighth	0	1	1	1	6	4	5	3	3	5	10	11	8	7	5	6	4	6	4	3	2	1
Ninth	1	0	1	1	8	7	3	5	5	7	3	6	8	7	6	6	5	3	4	2	4	4
Tenth	0	0	0	0	10	8	3	7	11	7	3	6	4	7	3	2	3	3	4	2	7	6
Eleventh	0	0	0	0	7	10	3	1	5	7	1	2	1	5	1	0	0	1	10	7	20	15

Capítulo II

CAPÍTULO III: Fine scale determinants of butterfly species richness and composition in a mountain region: implications for global change.

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Cover photograph: Male individual of *Gonepteryx rahmni* recorded in the transect “El Palancar”. Photo: Javier Gutiérrez Illán.

ABSTRACT

Aim Global patterns of species richness are often considered to depend primarily on climate. We aimed to determine how variation in topography and land cover affect species richness and composition at finer scales, and thus influence species diversity responses to climate change.

Location Sierra de Guadarrama (central Iberian Peninsula)

Methods We sampled the butterfly fauna of 180 locations (89 in 2004, 91 in 2005) at 600-2300 m elevation in a 10800 km^2 region. We recorded environmental variables at 100 m resolution using GIS, and derived GLMs for species density (number of species per unit area) and expected richness (number of species standardised to number of individuals) based on variables of *topoclimate* (elevation and insolation) or *habitat* (land cover, geology and hydrology), or both (*combined*). We evaluated the models against independent data from the alternate year. We also tested for differences in species composition among sites and years using constrained ordination, canonical correspondence analysis (CCA), and used variation partitioning analyses to quantify the independent and combined roles of topoclimate and habitat.

Results Topoclimatic, habitat and combined models were significantly related to observed species density and expected richness. Topoclimatic and combined models outperformed models based purely on habitat variables, showing a humped elevational diversity gradient. Both topoclimate and land cover contributed to accurate models of species composition.

Main conclusions Topoclimatic factors likely dominate species richness patterns in regions with pronounced elevational gradients, as long as large areas of natural habitat remain. In contrast, both topoclimate and land cover may have important effects on species composition. Continued conservation of natural habitat will be essential to protect rare species, facilitate range shifts, and avoid marked changes to species composition. Furthermore, a humped elevational diversity gradient implies that warming will reduce regional species richness as species distributions shift to higher elevations.

Keywords Elevational diversity gradient, lepidoptera, Mediterranean mountains, rarefaction, species composition, species richness-energy, variance partitioning.

INTRODUCTION

There is increasing evidence for changes to the distribution and abundance of species which are consistent with recent global warming (e.g. Parmesan & Yohe, 2003; Parmesan, 2006). At the individual species level, species distribution models play an important role in adapting conservation measures to climate change (Guisan & Thuiller, 2005). At a community level, the analysis of species richness gradients is critical for projecting how climate change may affect current assemblages and thus for developing conservation strategies (Fleishman et al., 2000). However, the validity of species richness models as tools for predicting future species assemblages may be limited, because the importance of climatic factors in determining species richness varies with spatial scale (grain and extent) (e.g. Rahbek, 2005, Field et al., 2009): at large spatial scales most available evidence suggests that climate/productivity gradients have the strongest correlations with species richness, whereas at smaller spatial scales the patterns are less clear-cut (Field et al., 2009). Much of this scale effect may result from of the levels of variation in climate and other factors included in studies, because (1) studies at small extents usually cover a relatively small climatic range, and (2) variation in other factors affecting species richness may average out to a greater degree than climate at large spatial scales (Field et al., 2009). Thus, climatic variables might still exert a dominant role at relatively small spatial scales in areas showing a large climate range, such as mountains (e.g. Stefanescu et al., 2004). However, in the case of the relatively mountainous Iberian Peninsula, for example, most studies have focused on how species richness is associated with certain types of habitat (e.g. Molina & Palma, 1996; Viejo et al., 1998; but see Stefanescu et al., 2004). In such locations, information on the effects of climate and additional factors (e.g. land cover) may be crucial for modelling species richness and its responses to environmental change.

During recent years, an increasing number of studies have discussed the relative importance of climate vs. habitat in determining individual species distributions (Pearson et al., 2004; Thuiller et al., 2004; Virkkala et al., 2005; Luoto et al., 2006; Parviainen et al., 2008). This debate has also extended to the community level, particularly in the context of species richness gradients and confronting the relative roles of energy vs. habitat heterogeneity (Kerr et al., 2001; Jiménez-Valverde & Lobo, 2007). However, whereas individual species distribution models are routinely cross-validated with independent data sets (Thuiller et al., 2004; Luoto et al., 2006; Parviainen et al., 2008), species richness models are rarely evaluated in this way (Kerr et al., 2001; Stefanescu et al., 2004; Kaboli et al., 2006; Menéndez et al., 2007; Kumar et al., 2009; but see Mac Nally et al., 2003; Hortal et al., 2004). This is an important limitation of many species richness models because successful model validations are required for models to be applied with confidence (Fielding & Bell, 1997; Olden & Jackson, 2000). In addition, most community level studies have concentrated on species richness, and rarely on species composition, a community attribute which also varies as a function of sampling grain and spatial extent (see Mac Nally et al., 2004; Kaboli et al., 2006). To provide a more complete picture of the possible implications of climate change for species assemblages, models for both species richness and species composition should be generated, as well as robust tests for the ability of these models to predict such community attributes at independent locations.

In this study, we examine the relative roles of topoclimatic and habitat variables for predicting the species richness and composition of butterfly assemblages in a mountain range in central Spain (Sierra de Guadarrama), which represents a hotspot of butterfly diversity (Van Swaay

& Warren, 2003). In this region, mean annual temperatures rose c. 1.3°C between 1967-73 and 1997-2003 (equivalent to an uphill shift in isotherms of c. 225 m) (Wilson et al., 2005). Over the same time, butterfly communities with comparable species compositions shifted upwards by 293 m (with richness generally declining) (Wilson et al., 2007), leading us to infer that climate was a key driver of species richness and composition, and that butterfly assemblages responded to climate warming with a negligible time delay. By analysing standardised butterfly data collected at distinct sites in 2004 and 2005, we now examine whether current species assemblages can be modelled using topoclimatic variables, or whether habitat factors have an important additional role. In addition, by using data from the alternate year, we are able to perform robust cross-validation tests for models of species richness and composition.

METHODS

Study system

The study system includes 10800 km^2 of the central Iberian Peninsula, with the south-west corner at 40º20'N 4º40'W (UTM reference 30TUK8050) and the north-east corner at 41º28'N 3º36'W (UTM 30TVL7070). The region consists of plains with elevations of ≥500 m (in the south) and ≥700 m (in the north), separated by the Sierra de Guadarrama, a mountain system with a maximum elevation of 2430 m.a.s.l. (Fig. 1). The region's climate is diverse, predominantly influenced by elevation and the complex topography. Dominant vegetation types are evergreen sclerophyllous woodland (largely *Quercus rotundifolia*) at elevations below 1000 m, deciduous woodland (largely *Quercus pyrenaica*) at roughly 1000-1500 m, and coniferous woodland (*Pinus sylvestris*) at approximately 1500-2000 m. Scrub and open grassland are present at all elevations, including beyond 2000 m (Rivas-Martínez *et al.*, 1987).

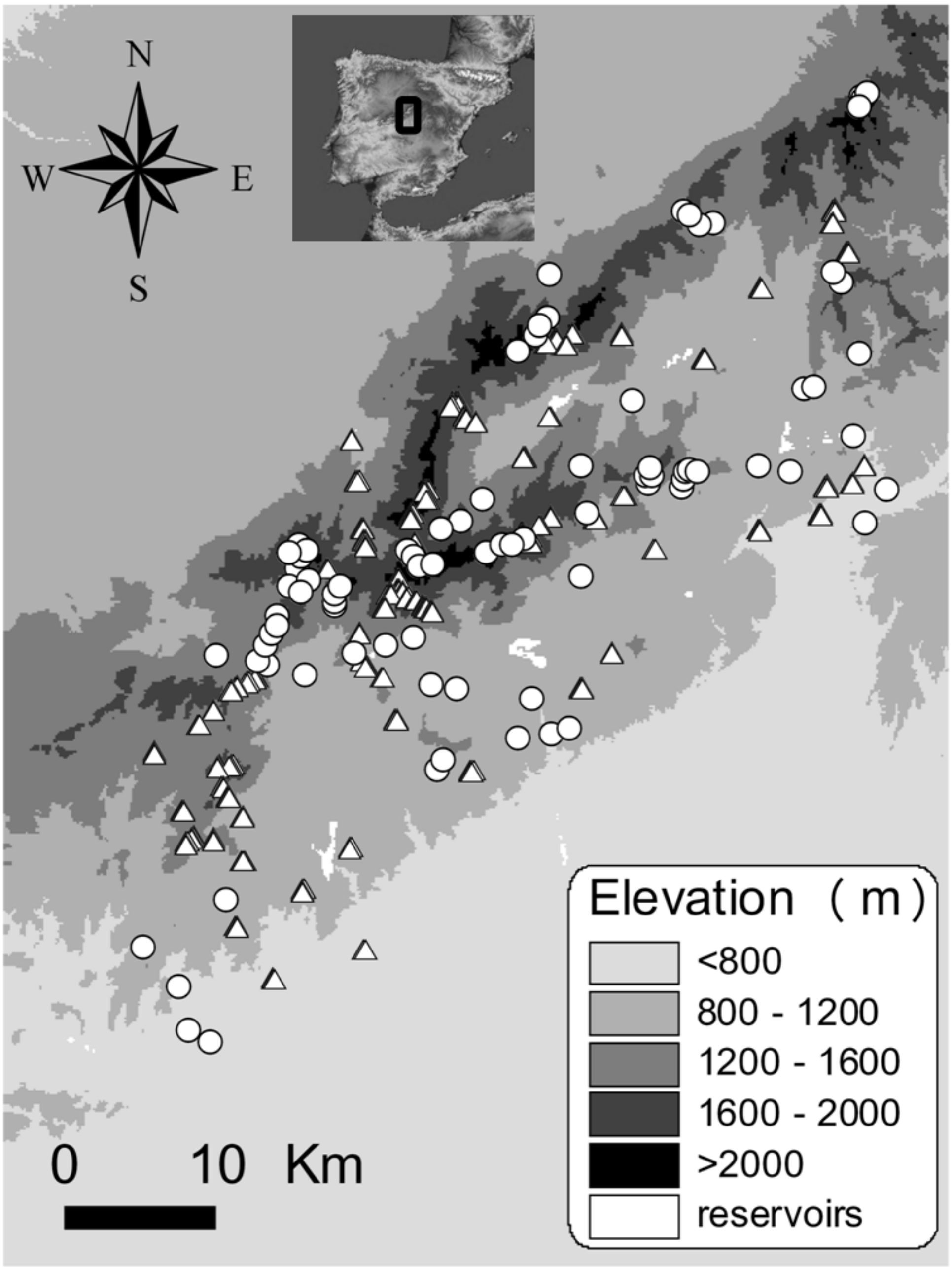


Figure 1 Map of the Sierra de Guadarrama showing elevation and sample sites. Elevation is shown in 400 m bands from <800 m (pale grey) to >2000 m (black). Sample sites are triangles (2004) and circles (2005).

Butterfly data

The fieldwork was conducted in the Sierra de Guadarrama and surrounding areas. Survey sites were accessible open areas of natural or semi-natural habitat (usually woodland clearings, scrub or pasture), stratified by elevation and selected to be representative of the main land cover types in the region. Butterflies were sampled at 89 sites in 2004 (elevational range 651-2260 m), and 91 independent sites in 2005 (elevational range 596-2303 m). In both surveys, butterflies were counted on standardised 500 m long x 5 m wide transects during suitable conditions for butterfly activity (Pollard & Yates, 1993). Presence/absence and abundance data were taken from four transects at each site between May and August (approximately every three weeks during the main butterfly flight period). Species abundance at each site was the sum count from four visits, and species were considered present if at least one individual was observed. We were not able to distinguish the individuals of three genera (*Carcharodus*, *Mellicta* and *Pyrgus*) in the field, so we pooled the species in each of these three genera for analyses. The total number of species for each location was the sum of species recorded for the four visits per year.

Spatial autocorrelation can influence the reliability of biogeographic analyses, particularly for samples separated by short geographic distances (Algar *et al.*, 2009). Survey sites in each 400 m elevation band were represented in different parts of the study region, and in separate 1 km grid squares. Mean distance between nearest neighbouring sites was 2.2 km ± SE 0.2 in 2004, and 1.9 km ± SE 0.2 in 2005. In practice, the geographically closest sites (at high elevations, where potential sample sites were limited) were widely separated in elevation; and at lower elevations most sites were much further apart. To detect spatial autocorrelation in our data, we calculated Geary's *c* coefficient (Geary, 1954) for 2004 and 2005 species density and expected species richness at each site (see Data Analysis and Modelling). Geary´s *c* is recommended instead of Moran´s *I* when the response variable is not normally distributed (Schofield *et al.*, 2007; Maestre *et al.*, 2008), because it takes into account the differences between observed values in two different sites, without using the average value of the response variable (Fortin & Dale, 2005). Geary´s correlograms for 2004 and 2005 data showed no significantly spatially autocorrelated values of species density and expected richness from samples of 13 and 52 individuals (P >0.01), considering the 89 and 91 sites, respectively.

Environmental data

Universal Transverse Mercator (UTM) coordinates were estimated to the nearest metre at least every 100 m along each transect using a handheld Garmin GPS unit in the field. The coordinates were used to plot each transect in ArcGIS 8.1 (ESRI, 2001). Environmental layers were obtained from three sources: (1) a digital elevation model of the area shown in Fig. 1, which was obtained at 80 x 80 m resolution and interpolated to 100 x 100 m (NASA/JPL-Caltech 2004); (2) regional land cover maps obtained in vector format at 1:50000 scale (CAM, 1998; Ministerio de Medio Ambiente, 2000, 2002a b, 2003), which showed good agreement for all transects with our own field observations of general vegetation type; and (3) a regional geology map also obtained in vector format (SIEMCALSA, 2001). All variables were available in digital format and could be quantified over large spatial scales, even in locations in which no butterfly inventories were conducted. Vector data from the land cover and geology maps (minimum cartographic unit 2.25 ha) was used to determine the proportion contribution of each land cover or geology type to each 100 m grid cell. Each environmental variable was measured for each transect as the average for 100 m grid squares intercepted by the transect.

Environmental variables were classified as relating either to “topoclimate” or “habitat”. Topoclimatic variables were all derived from the 100 m digital elevation model, and included elevation (m), its square term for potential unimodal responses of butterfly diversity (Jiménez-Valverde & Lobo, 2007), and estimated solar radiation for the summer and winter solstices (kWh/m^2), which has been shown to be important for butterfly diversity (Kerr et al., 2001). Annual mean temperature decreases by ca. 5.8-5.9°C, and annual rainfall increases ca. 683-767 mm per 1000 m elevation increase in the study area (relationships with $r^2 > 0.90$ for 1967-1973 and 1997-2003; Wilson *et al.*, 2005). These climatic gradients are based on a limited number of meteorological stations, hence we used elevation and modelled insolation intensity instead of estimated temperature and rainfall in our models. Solar radiation parameters were obtained by implementing the *Solar analyst* tool (Fu & Rich, 2000) in ArcView 3.1, which estimates the incoming radiation to a grid cell using the slope, aspect, curvature, elevation and shading effects from surrounding topography. Slope, aspect and curvature were not included as additional topoclimatic variables since their effects are included in the estimates of solar radiation.

We first grouped land cover types as corresponding to the major classes of evergreen broadleaf forest, deciduous broadleaf forest, coniferous forest, shrubland, meadows / pasture, juniper forest, bare rock, crops, or artificial (human infrastructure, reservoirs, etc). Classes which were present on fewer than 10% of transects were not included as independent variables in the analyses, leaving a final variable list of deciduous forest, coniferous forest, shrubland and meadows / pasture. We calculated a "total forest" variable as the combination of "coniferous" plus "deciduous" plus "evergreen broadleaf" plus "juniper", to account for species broadly associated with tree cover. The land cover map was also used to calculate mean river length (in km) in each 100-m grid cell intercepted by each transect. We grouped geological data into the broad classes of metamorphic rocks (predominantly gneiss), granites, and limestone. Limestone was present on only 8 transects and was not included as an explanatory variable. Cover of metamorphic rocks and granites were strongly negatively correlated (Spearman rank correlation coefficient, $r_s = -0.932$, $P < 0.001$), and so only one (metamorphic rock) was included as an environmental variable. Of the final variables selected for analysis, none were highly correlated (absolute values of $r_s < 0.5$) apart from elevation and its square term. The final set of explanatory environmental variables is listed in Table 1.

Table 1 List of environmental variables included in the analyses

Environmental variable	Code	Mean (min-max)
a) Topoclimatic variables		
Elevation (km)	ELEVN	1.443 (0.596-2.303)
Elevation^2 *	ELEVN2	
Winter solstice insolation intensity (kWhJ/m^2)	WINTER	0.728 (0.064-1.373)
Summer solstice insolation intensity (kWh/m^2)	SUMMER	5.171 (4.554-5.694)
b) Land cover variables		
Deciduous forest (proportion cover)	DECID	0.106 (0-1)
Coniferous forest (proportion cover)	PINE	0.277 (0-1)
Total forest (proportion cover)	FOREST	0.462 (0-1)
Shrubland (proportion cover)	SHRUB	0.313 (0-1)
Pasture / meadows (proportion cover)	MEADOW	0.130 (0-1)
Metamorphic rock (proportion cover)	GNEISS	0.499 (0-1)
River length (length in km)	RIVER	0.01 (0-0.96)

* Not included in species composition analyses

Data analysis and modelling

Species density and richness

To distinguish species density from actual species richness is important when assemblages differ strongly in total abundance (McCabe & Gotelli, 2000). Most studies of species diversity are standardised on the basis of area or sampling effort, and therefore describe species density per unit area or sample rather than species richness (Gotelli & Colwell, 2001). In our study, we counted species for four visits per transect, which represents a measure of species density. In contrast, species richness comparisons should be made by standardising data sets to a common number of individuals. To estimate standardised species richness we used rarefaction curves representing the means of repeated re-sampling of all pooled individuals for each site (Gotelli & Colwell, 2001). We used a Monte Carlo method to estimate the expected species richness for a given number of individuals drawn randomly from a sample using *Ecosim* simulation software (Gotelli & Entsminger, 2001). The site with the lowest overall butterfly abundance had 13 individuals. Therefore, we randomly sampled 13 individuals for each site and recorded the number of species. We repeated each randomisation 1000 times for each site and then we used the mean number of species as the expected species richness (response variable) in the analyses (Gutiérrez & Menéndez, 2007). Because 13 individuals is a rather small sample size, we repeated the modelling using samples of 52 individuals (the maximum number of species observed in a site). In this case we had to exclude four and nine sites from 2004 and 2005 respectively, because the total number of individuals recorded were lower than the threshold value.

To test the effects of both topoclimate and habitat variables on butterfly diversity in the study area, we performed stepwise generalized linear models (GLMs) against the eleven predictors, with species density and expected species richness as response variables (Legendre & Legendre, 1998). Because the distribution of the response variable is a count ranging from zero to the maximum number of individuals sampled at a site, we applied a quasi-likelihood estimation of the regression coefficients using a log-link to avoid over-dispersion, and setting the variance equal to the mean (Venables & Ripley, 1997; MathSoft, 1999). Model selection was performed with S-plus (Version 6.1 for Windows, Insightful Corp.) using a forward QAICc-based procedure until no additional terms improved the model. The QAICc is a modified version of Akaike´s information criterion for model selection which corrects for small sample size relative to the number of estimated parameters and for an overdispersion factor (Burham & Anderson, 2002). To test for the contribution of different types of variables, separate GLMs were constructed with topoclimatic and habitat variables, and a third GLM with all the explanatory variables: these define the three types of models, named hereafter topoclimate, habitat and combined models, respectively. Each type of model was derived separately for the 2004 and 2005 sites (hereafter, model “calibration”).

Models were evaluated by two methods. The first method (verification) was based on plotting the observed response values (species density or expected richness) used for calibration against the values predicted by the model. The second method was a cross-validation test carried out using 2004 models to predict the response variables at the independent locations in 2005, and vice versa. Model performance (verification and cross-validation) was tested using Spearman's non-parametric correlation coefficient (r_s) (see Thomson *et al.*, 2007). The three models for each year were used to plot predicted species density and expected richness maps in GIS for the entire study area, based on environmental variables.

Variation partitioning is commonly used to extract the variance explained by groups of factors in a series of models (Borcard et al., 1992). Variation partitioning was used here to decompose the variation in species diversity among the two types of variables, topoclimatic (T) and habitat (H). We used the variables selected in the forward selection performed in combined model calibration, and conducted variation partitioning using the "vegan package" implemented in R version 2.1.0 (R Development Core Team, 2005). Variation partitioning in our study led to four fractions: (i) effect of pure topoclimate models (fraction *a*); (ii) effect of pure habitat models (fraction *b*); (iii) combined variation due to joint effects of topoclimate and habitat (fraction *c*) and (iv) unexplained variation (fraction U).

Species composition

To identify the variables related to species composition among sites we used constrained ordination, canonical correspondence analysis (CCA), performed by CANOCO software (ter Braak, 1986). We checked the appropriateness of CCA (which assumes a unimodal response of species abundance) by performing a preliminary detrended correspondence analysis (DCA) with detrending by segments, which provides an estimate of the length of the extracted axes in units of standard deviation (SD). As the first axes were 3.48 (for 2004) and 4.21 (for 2005)

SDs in length, greater than the threshold range (1.5–3 SDs) recommended for performing unimodal methods (ter Braak & Prentice, 1988), we confirmed the appropriateness of CCA for our data set. First, we performed a CCA on the species-samples matrix including the full set of environmental variables. We developed three types of models depending on the variables included, as for species density and richness analyses; topoclimatic, habitat and combined models. Because not all variables could have a significant influence on the species composition matrix, we proceeded to generate reduced models using a forward stepwise selection of the environmental variables. The statistical significance of the models was evaluated by the F-ratio based on the trace and 4999 unrestricted Monte Carlo permutations. After the forward selection procedure, we calculated corrected *P*-critical values using the sequential Bonferroni's correction (Rice, 1989). We then added variables until no additional terms improved the model following the sequential Bonferroni's correction.

We evaluated model performance using cross-validation tests. We extracted sample scores of each ordination axis obtained from CCA analyses, first using 2004 sites as active samples and setting 2005 sites as supplementary samples ("passive samples" in earlier versions of CANOCO), and then vice versa. Using supplementary samples consists of making some samples passive in the analyses, so that these samples do not influence the ordination axes but are added afterwards, and therefore their relation to the other samples can be judged from their position in the ordination analysis (ter Braak & Smilhauer, 2002). Therefore, we obtained sample scores for each year based on the other year's dataset, without the former year influencing the ordination axes. Performance of 2004 models was then tested using Spearman's non-parametric correlations of sample scores for the 91 sites in 2005 used as supplementary samples (independent data) and 2004 sites as active samples (the models) against sample scores of 2005 sites when set as active samples ("observed" data), and vice versa for the 2005 models using the 89 sites in 2004.

Variation partitioning was also used here to decompose the variation in species composition among topoclimatic and habitat variables, using a series of (partial) canonical correspondence analyses implemented in CANOCO version 4.5. Because we were working in a unimodal context (CCA), we divided the the sum of all canonical eigenvalues by the sum of all eigenvalues of the species matrix to obtain the percentage of explained variation (Borcard et al., 1992). Variation partitioning led to the same four fractions as for species density and expected species richness.

RESULTS

Field survey

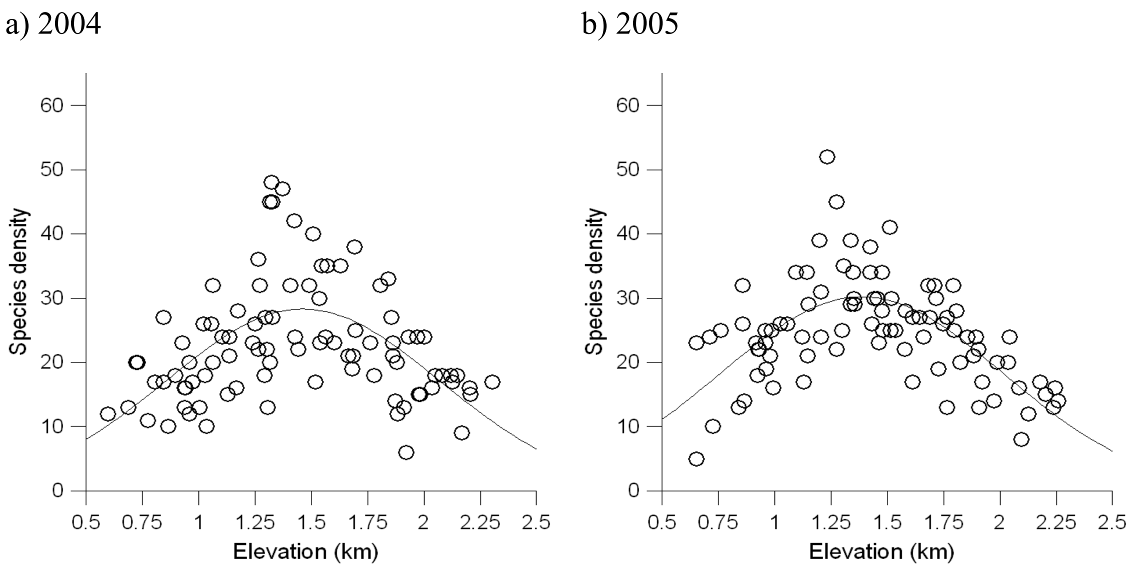
We recorded 95 species in 2004 and 93 in 2005, plus three genera not identified to species level in both years. We recorded a total of 21831 individuals in 2004 (89 locations) and 16844 individuals in 2005 (91 locations). The relative prevalence (proportion of sites occupied) of the 92 species that were present in both years was strongly positively correlated between 2004 and 2005 ($r_s = 0.87$, $P < 0.001$, $n = 92$).

Species density and richness

Models containing at least one environmental variable were obtained for the three types of models (topoclimatic, habitat and combined) in both years, for species density and for expected species richness from samples of 13 and 52 individuals. The coefficients of each variable included in each type of model are listed in Tables 2 and 3. Elevation was the most selected variable, showing a unimodal relationship with species density (positive effect of elevation; negative effect of elevation^2) in 2004 and 2005, both in topoclimatic and combined models (Table 2) with a peak in species density at mid-altitudes (Fig. 2). We found the same unimodal relationship for expected species richness from samples of 13 and 52 individuals both in 2004 and 2005 (Table 3). Of the habitat variables, river length, metamorphic rock and shrubland were selected most frequently in habitat and combined models, each with consistent positive effects (Tables 2 and 3). To asses the consistency of the predicted values, we performed correlations of modelled species density and expected species richness for 2004 and 2005, and in all cases they were highly significant ($P < 0.001$).

Table 2 Coefficients of variables for models of species density, and model evaluation (verification and cross-validation) using Spearman's correlation coefficients. Top: topoclimatic; Hab: habitat; Comb: combined. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

	2004			**2005**		
Variables	Top	Hab	Comb	Top	Hab	Comb
Intercept	-1.39	2.61	-1.57	0.44	2.68	0.32
ELEVN	3.50		3.15	3.98		3.83
ELEVN2	-1.33		-1.22	-1.36		-1.29
WINTER						
SUMMER	0.49		0.54			
DECID					0.42	0.47
PINE						
FOREST		0.71	0.13		0,39	0.49
SHRUB		0.44			0.27	
MEADOW		0.57				
GNEISS			0.13		0.15	0.17
RIVER		3.18	3.22		4.66	4.55
Verification	0.73^{***}	0.50^{***}	0.73^{***}	0.63^{***}	0.43^{***}	0.70^{***}
Cross-validation	0.54^{***}	0.30^{**}	0.63^{***}	0.65^{***}	0.36^{***}	0.59^{***}


a) 2004

b) 2005

Figure 2 Unimodal relationships of elevation with species density in (a) 2004 and (b) 2005, fitted using a Poisson error distribution. Sampling sites shown as empty circles. The lines of best fit represent the equations: a) Species density = *exp* (0.96 + 3.53 elevation – 1.27 elevation^2); b) Species density = *exp* (0.44 + 3.98 elevation – 1.36 elevation^2).

Table 3 Coefficients of variables for models of expected species richness and model evaluation (verification and cross-validation) using Spearman's correlation coefficients. Results are presented for expected species richness based on random samples of 13 and 52 individuals from each site (see materials and methods for further details). Top: topoclimatic; Hab: Habitat; Comb: combined. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	13 indiv threshold						**52 indiv threshold**					
	2004			**2005**			**2004**			**2005**		
Variables	Top	Hab	Comb	Top	Hab	Comb	Top	Hab	Comb	Top	Hab	Comb
Intercept	0.97	1.82	0.90	1.09	1.98	1.10	1.23	2.42	1.62	1.24	2.74	1.25
ELEVN	1.47		1.55	1.29		1.27	2.15		2.15	2.12		2.07
ELEVN2	-0.49		-0.52	-0.43		-0.43	-0.72		-0.73	-0.70		-0.68
WINTER												
SUMMER												
DECID		0.25						0.39	0.10			
PINE		0.23						0.35				
FOREST												
SHRUB		0.25	0.11					0.37	0.16			
MEADOW		0.17			-0.10			0.24			-0.22	
GNEISS					0.06	0.06						
RIVER			1.91					1.66	2.54		1.77	1.67
Verification	0.44^{***}	0.38^{***}	0.50^{***}	0.46^{***}	0.20^{*}	0.49^{***}	0.56^{***}	0.50^{***}	0.63^{***}	0.55^{***}	0.30^{**}	0.56^{***}
Cross-validation	0.46^{***}	0.13^{ns}	0.43^{***}	0.44^{***}	0.11^{ns}	0.43^{**}	0.54^{***}	0.29^{**}	0.54^{***}	0.55^{***}	0.10^{ns}	0.57^{***}

Model performance was evaluated using Spearman's non-parametric correlation coefficient. In model verification, r_s values ranged from 0.43 to 0.73 for species density (Table 2). For expected species richness, r_s values ranged from 0.20 to 0.50 for samples of 13 individuals, and from 0.30 to 0.63 for samples of 52 individuals (Table 3). In all cases, r_s for habitat models were lower than those for topoclimatic models, which in turn were lower than those for combined models.

In model cross-validation, r_s values ranged from 0.30 to 0.65 for species density (Table 2), from 0.11 to 0.46 for expected richness based on samples of 13 individuals, and from 0.10 to 0.57 for samples of 52 individuals (Table 3). In all cases r_s for habitat models were lower than those for topoclimatic and combined models. There was no clear difference between cross validation r_s values for topoclimatic and combined models. Maps predicting species density for the entire study system are shown in Fig. 3.

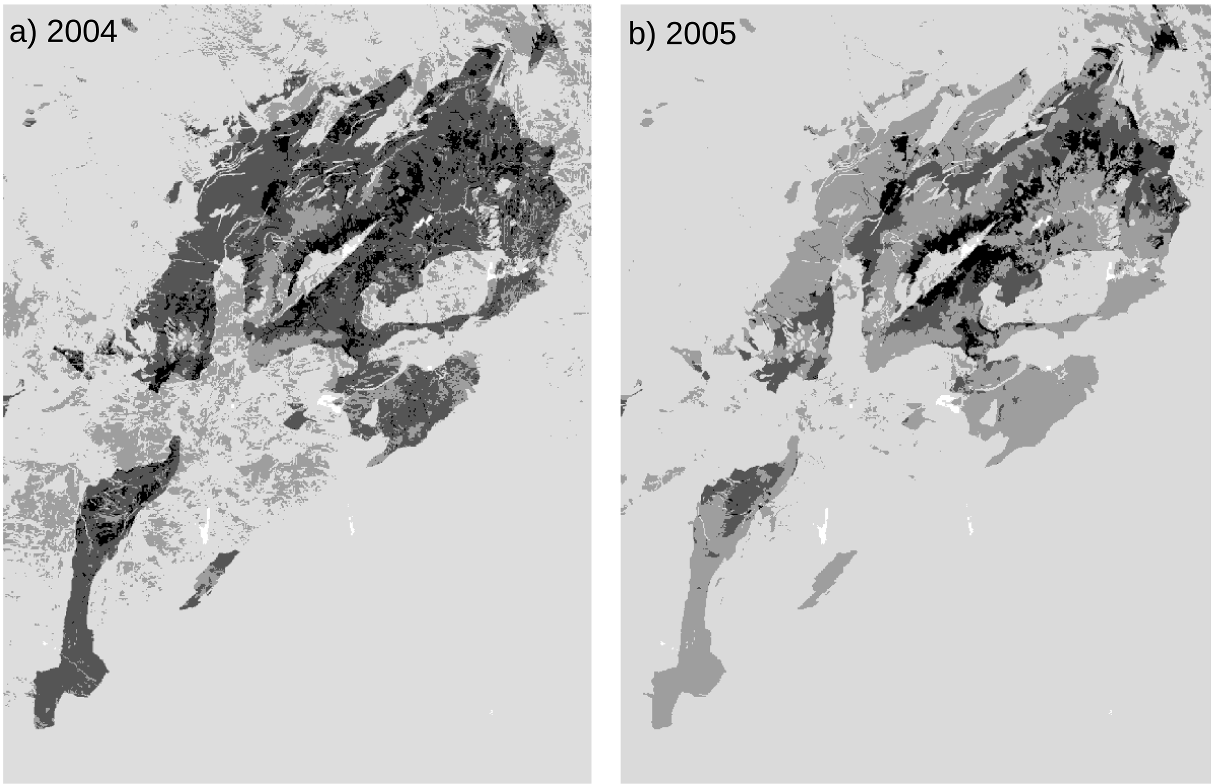


Figure 3 Predictive maps for species density in the study area. Maps for (a) 2004 and (b) 2005 combined models show predicted species density from pale grey (0-10 species), to black (>30 species). Study area, spatial scale and regional context identical to Fig.1. Reservoirs are shown in white.

Results of variance partitioning analyses for species density are shown in Fig. 4. In both study years, combined models explained similar variation in species density (44.6% in 2004 and 48.4% in 2005). In 2004, the unique effects of topoclimatic and habitat variables were smaller than in 2005. However, in both cases the unique effects of topoclimatic variables were greater than those of habitat variables. Results for variation partitioning analyses for expected species richness from 13 and 52 individuals showed the same patterns (results not shown)

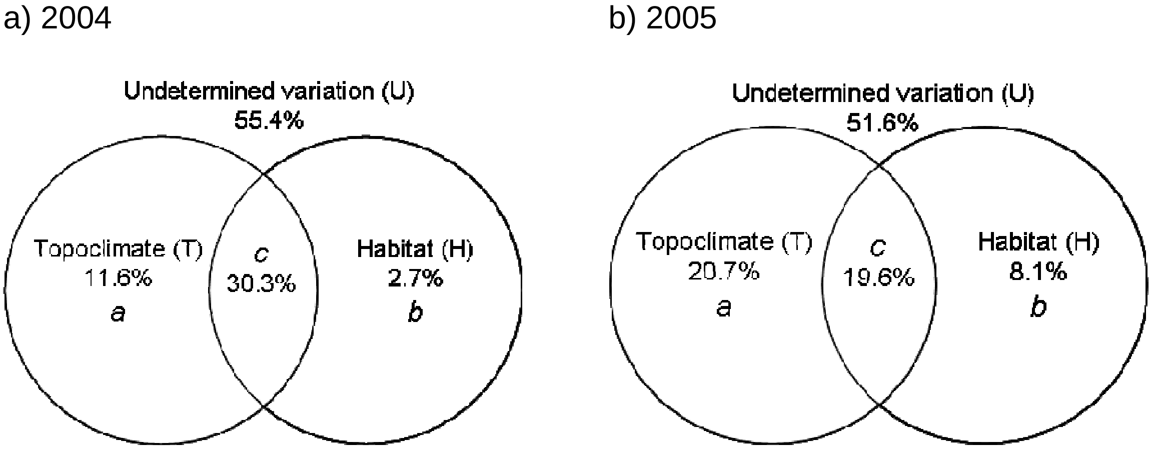


Figure 4 Results of variation partitioning for butterfly species density in (a) 2004 and (b) 2005 in terms of fractions of variation explained. Variation of species density is explained by two groups of variables: T (topoclimatic), H (habitat), and U is the unexplained variation. Unique effects of topoclimatic and habitat factors are represented by fractions *a* and *b*, respectively, while fraction *c* represents their joint effects.

Species composition

In CCA with the full set of topoclimatic variables the first four axes explained 16.4% of the variance in 2004 and 16.2% in 2005. Using forward stepwise selection, a reduced set of topoclimatic variables (including one variable in 2004 models and two in 2005) explained 13.2% of the variance in 2004 and 14.8% in 2005 (Table 4). When using only habitat variables, a reduced set of variables significantly explained 14.9% of the variance in species composition in 2004 and 17.8% in 2005 (Table 4), out of 20.5% and 21.3% respectively for the full set of seven habitat variables. In combined models, a reduced set of both types of variables significantly explained 21.0% of the variance in species composition in 2004 and 22.1% in 2005 (Table 4), out of 29.4% and 31.4% respectively for the full set of ten variables.

Table 4 Eigenvalues and cumulative explained variance (%) of species composition explained by topoclimatic, habitat and combined models. Results are shown for the first four axes obtained by CCA using the reduced set of environmental variables selected by stepwise procedure in each type of model.

Analysis		**Axis**				***F***	***P***
		1	**2**	**3**	**4**		
Eigenvalues							
2004	Topoclimatic	0.461	-	-	-	13.268	<0.001
	Habitat	0.282	0.145	0.056	0.036	3.685	<0.001
	Combined	0.465	0.158	0.066	0.042	5.577	<0.001
2005	Topoclimactic	0.541	0.084	-	-	7.666	<0.001
	Habitat	0.380	0.183	0.115	0.070	3.402	<0.001
	Combined	0.564	0.232	0.086	0.049	5.025	<0.001
Cumulative explained variance (%)							
2004	Topoclimatic	13.2	-	-	-		
	Habitat	8.1	12.3	13.9	14.9		
	Combined	13.3	17.9	19.8	21.0		
2005	Topoclimatic	12.8	14.8	-	-		
	Habitat	9.0	13.4	16.1	17.8		
	Combined	13.4	18.9	20.9	22.1		

The F-test and significance (after 4999 Monte Carlo permutations) for each model are also shown.

Results obtained for ordination axes were broadly concordant in 2004 and 2005 models in all cases. In topoclimatic models for 2004 there was only one axis (one variable selected - elevation), and two for 2005 models (elevation and winter insolation) (Table 5). In habitat and combined models for 2004 and 2005, a range of variables were selected: deciduous forest, shrubs and coniferous forest had significant effects on habitat models in both years and elevation and coniferous forest had significant effects in combined models in both years (Table 5).

Table 5 Intra-set correlations of environmental variables with the first four ordination axes of the CCA analyses in each type of model (topoclimatic, habitat, combined). Correlations with absolute values greater than 0.5 are shown in bold.

Type of model		Variables	*F*	*P*	Axis			
					1	2	3	4
2004	Topoclimatic	ELEVN	13.27	<0.001	**1.000**	-	-	-
	Habitat	DECID	2.23	0.001	0.133	-0.373	0.460	**0.795**
		SHRUB	5.35	<0.001	-0.417	**0.863**	0.284	0.031
		MEADOW	2.19	0.001	0.496	-0.172	**0.554**	**-0.646**
		PINE	5.07	<0.001	**-0.719**	-0.479	-0.416	-0.285
	Combined	ELEVN	13.27	<0.001	**0.995**	0.002	0.099	-0.008
		DECID	2.39	<0.001	-0.131	-0.230	0.436	**0.860**
		SHRUB	1.92	0.002	0.410	**0.578**	**-0.644**	0.287
		PINE	3.76	<0.001	0.437	**-0.766**	-0.222	-0.416
2005	Topoclimatic	ELEVN	12.98	<0.001	**0.995**	-0.104	-	-
		WINTER	2.18	0.002	0.054	**-0.999**	-	-
	Habitat	DECID	2.19	0.002	0.360	0.464	-0.388	0.270
		SHRUB	3.41	<0.001	0.074	**-0.673**	-0.311	**-0.505**
		PINE	6.33	<0.001	**-0.798**	0.362	0.264	-0.117
		FOREST	2.49	0.003	-0.357	**0.693**	0.391	0.049
		GNEISS	2.99	<0.001	**-0.662**	-0.142	0.128	**0.570**
		RIVER	1.96	0.006	-0.381	**0.545**	0.215	-0.001
	Combined	ELEVN	12.98	<0.001	**0.962**	0.242	-0.104	0.027
		WINTER	2.30	<0.001	0.060	-0.072	**-0.950**	0.246
		PINE	5.49	<0.001	0.485	**-0.781**	0.111	-0.120
		FOREST	2.90	0.001	0.099	**-0.762**	0.351	0.492
		RIVER	1.89	0.006	0.127	**-0.684**	-0.004	-0.240

Variables were selected with a stepwise procedure. Only significant variables after sequential Bonferroni's correction of the critical *P-value* were included. *P-value* shown in table is the uncorrected significance of the *F*-tests for each variable after 4999 Monte Carlo permutations.

The performance of species composition models for 2004 was evaluated by calculating r_s values between sample scores for the first four CCA ordination axes obtained for 2005 sites (used as supplementary samples with 2004 locations as active samples) and scores for 2005 sites as active samples, and vice versa for 2005 models. We obtained highly significant r_s values ($P < 0.001$) in 14 out of 18 cases (78%) (Table 6). Correlation coefficients were higher than 0.95 for the first axis (based largely on elevation in topoclimatic and combined models), and higher than 0.73 for the second axis in all cases, suggesting that species composition in this region can be predicted very accurately between years by the models. The significant negative r_s values obtained in some cases simply show that the ordination of the sites with respect to the axes is reversed, but the relative position of the sites does not vary.

Table 6 Cross-validations of the first four CCA ordination axes of (a) 2004 and (b) 2005 species composition models. Spearman´s correlation coefficients (r_s) between the sample scores obtained from CCAs of 2005 sites (defined as supplementary samples, with 2004 sites as active samples) against 2005 sites as active samples are shown (a), and viceversa (b). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Models		**Axis**			
		1	**2**	**3**	**4**
a) 2004	Topoclimatic	0.989***	-	-	-
	Habitat	0.954***	-0.824***	-0.540***	0.123^{ns}
	Combined	0.991***	0.808***	0.502***	0.592***
b) 2005	Topoclimatic	0.989***	-	-	-
	Habitat	0.976***	-0.732***	-0.578***	0.012^{ns}
	Combined	0.995***	0.865***	0.144^{ns}	0.210*

Results for variation partitioning analyses for species composition are shown in Fig. 5. In both study years, most variation was accounted for by unique effects from topoclimatic and habitat variables. In 2004, the amount of variation explained by each group of variables was identical (8.9%), whereas in 2005 topoclimatic variables accounted for slightly more variation in species composition than habitat variables.

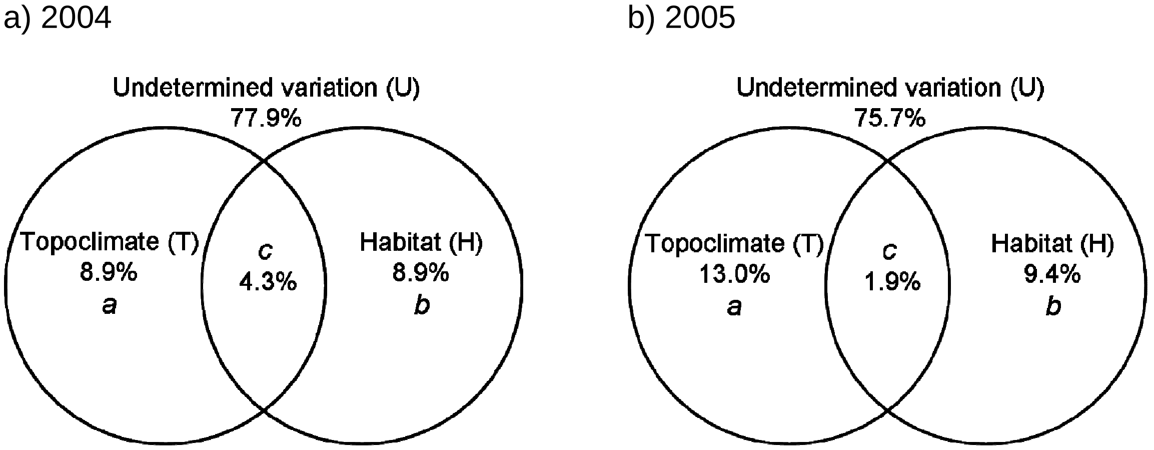


Figure 5 Results of variation partitioning for butterfly species composition in (a) 2004 and (b) 2005 in terms of fractions of variation explained. Variation is species composition is explained by two groups of variables: T (topoclimatic), H (habitat), and U is the unexplained variation. Unique effects of topoclimatic and habitat factors are represented by fractions *a* and *b*, respectively, while fraction *c* represents their joint effects.

DISCUSSION

Here we demonstrate strong effects of elevation on butterfly diversity in a mountain range, with some evidence for supplementary effects from other topoclimatic variables, and from river length, geology, and land cover. There was concordance in variable selection between models calibrated using different data sources (year 2004 vs. 2005), different response variables (species density, expected species richness, and species composition), and different statistical approaches (GLM and CCA vs. VP), supporting the consistency of our results. Concordance between standard modelling (GAM) and partitioning methods (HP) was found in another similar study (Luoto *et al.*, 2006). However, to our knowledge, this is the first study showing consistency between the results for models using diversity data from different years, possibly because most previous studies were based on presence data from atlas or similar sources combining data from several years.

Topoclimate versus habitat

Elevation appears to be the main determinant of butterfly species richness in this system, based on model evaluation for species density, expected richness from 13 and 52-individual samples, and from variance partitioning analysis (Tables 2, 3, Fig 4). The performance of models based on expected species richness was slightly lower than that of species density models, presumably due to the more restricted range of values of the response variable. At continental scales, climate variables appear to be the main determinants of butterfly diversity patterns (Kerr, 2001; Hawkins and Porter, 2003; Hawkins et al., 2003), whilst both topoclimate and land cover are important for predicting species richness and composition at finer scales (Kerr et al., 2001; Storch et al., 2003). In the Sierra de Guadarrama, the distribution and abundance of many butterfly species depend primarily on topoclimate rather than land cover (Gutiérrez Illán et al, in press): the current analyses show that this pattern translates to fine scale patterns of butterfly species richness in the system.

In contrast to the results for species richness, topoclimate and habitat variables explained similar fractions of the variation in species composition (Table 4, Fig 5), and cross-validation using sample scores in CCA revealed very high correlations both for topoclimate and habitat models (Table 6). Combined models explained the largest part of the variation in species composition in both years. The percentage of explained variance in species composition for the first four axes in the topoclimatic, habitat and combined models were only slightly smaller than those for the CCA including the full set of variables, suggesting that the reduced variable lists included relevant explanatory variables for species composition. Rather few variables (consistently elevation and pine forest cover) apparently explained a large proportion of the variation in species composition in this system. In variance partitioning, the joint effects of topoclimatic versus habitat predictors on species composition were much smaller than those obtained for species richness analyses (Figs 4, 5), suggesting that effects of topoclimate and habitat on species composition are more independent.

Ecological significance of the models

The dominant role of elevation in modelling species richness is likely due to the marked elevational gradient in the system, directly related to temperature, rainfall and other climatic factors, which in turn influence the physiology, life history and ecological processes of butterfly populations (Dennis, 1993). However, whereas at higher latitudes temperature availability limits regional-scale butterfly species richness (Turner et al, 1987; Menéndez et al., 2006, 2007), for many species there may not be a strong limitation of low temperatures at high elevations in Mediterranean mountains (although the length of the growing season may be reduced). In contrast, prolonged hot and dry conditions in the lowlands may represent a limiting factor, by influencing butterfly mortality directly (e.g. Merrill et al. 2008), or through effects on the condition of larval host plants.

Of the variables selected by habitat and combined models, there were consistent positive effects on butterfly species richness from deciduous forest, river length and metamorphic rock cover. Most deciduous forests occur at medium elevations where species diversity peaked, but deciduous woodland could have an additional positive effect by providing shaded areas where host plant senescence may be delayed (e.g., see Weiss et al., 1988). Increased humidity and water availability may also play a role in delaying summer droughting and desiccation of larval host plants and nectar sources (Murphy et al., 1983; Stefanescu et al., 2004), explaining the positive effect of river length. Our example, and another showing positive correlations of butterfly species richness with wet conditions in the Mediterranean (Stefanescu et al., 2004), show how local to regional species richness patterns can reflect the water-energy budget, just as they do at continental scales (Hawkins and Porter, 2003). The positive effect of acidic metamorphic rocks (gneiss) on butterfly diversity may be related to the distribution of larval host plants. As reported by van Swaay (2002), butterfly communities tend to be richer on basic soils, probably related to the distribution of larval host plants, which suggest that the dominance of acidic rocks could lead to reduce species diversity. There were few limestone sites in this system, but some butterfly host plants commonly associated with basic soils, such as *Hippocrepis*, a host plant for *Polyommatus* species (Lycaenidae), also occur on soils overlaying gneiss in the Sierra de Guadarrama (Fernández-González, 1991).

Species composition was affected by both topoclimate and habitat, in contrast to our results showing a dominant effect of topoclimate on species richness and individual species distributions (Gutiérrez Illán et al., in press). In part, this discrepancy could arise because the distributions of 48 relatively widespread species were modelled in Gutiérrez Illán et al. (in press). These species may have a major effect on species richness in the present study, but a total of 102 species, many of them rare, influence species composition. The environmental correlates of overall species richness may be of limited value for modelling the narrow distributions of rare species (Jetz & Rahbek, 2002). These localized species may be restricted to certain habitat types, increasing the importance of variables related to host plant or other resource distributions (e.g., land cover, geology and river length) in species composition analyses (Menéndez et al., 2007).

Elevational gradients in diversity

Models based both on species density and expected species richness revealed a dominant effect of elevation on butterfly diversity, with a strong humped elevational gradient (Fig. 2). Based purely on elevation, peak species density was estimated to occur at 1390 m (2004) to 1463 m (2005), in accordance with an estimate of peak richness at 1360 m from more intensively sampled sites in 1967-73 and 2004-05 (Wilson et al., 2007). Humped relationships of butterfly species richness with elevation have been shown in several other studies at comparable latitudes (Thomas & Mallorie, 1985; Fleishman et al., 1998; Stefanescu et al., 2004; but see Fleishman et al., 2000). Here the pattern could reflect a combination of unsuitably hot and dry conditions for many species at low elevations, and the absence of host plants or of favourable conditions for flight or reproduction at high elevations (e.g., see Dennis and Shreeve, 1989; Mac Nally et al., 2003; Merrill et al., 2008). Certainly many species have clear lower and upper elevational limits in the region, and rather few species are restricted to the lowest elevations (Wilson et al., 2005, 2007; Gutiérrez Illán et al., in press).

Elevational diversity gradients may be confounded by patterns of human disturbance and land use, which are usually more intensive at low altitudes (McNeill, 1992; Rahbek, 1995; Nogués-Bravo et al., 2008). Although this is likely the case to some extent for the current system, rather large areas of natural and semi-natural habitat remain at all elevations, suggesting that diversity patterns may represent robust relationships of butterfly diversity with temperature and productivity.

Global change effects on diversity

The models here represent a first step in identifying the determinants of species richness and composition in a region of high butterfly diversity. Elevation plays a particularly important role, almost certainly because of the influence of elevation on temperature, rainfall and other climatic variables, which affect butterfly survival and fecundity both directly and through their effects on interacting species such as larval host plants. At present, land cover appears to have a subsidiary effect on species richness, although its effect on species composition seems to be stronger, perhaps through effects on the distributions of resources for rare species (e.g., see Menéndez et al., 2007). Comparison of elevational patterns in species richness and composition between 1967-73 and 2004-05 suggest that the component species of butterfly communities have shifted their distributions uphill at similar rates in this system (Wilson et al., 2007), probably because of marked climate variation over short distances, and because large areas of natural and semi-natural habitat remain. Such a scenario contrasts with the pronounced recent changes to butterfly communities in more fragmented environments at higher latitudes, where dispersive generalists have expanded their distributions related to climate change but habitat specialists have shown range contractions because of habitat loss (Warren et al., 2001; Menéndez et al., 2006; White and Kerr, 2007). In the face of climate change, continued protection of natural habitats in mountain systems like the Sierra de Guadarrama will be critical to conserve rare species, facilitate range shifts, and avoid changes to species composition.

The humped elevational gradient in butterfly diversity reported here and in Wilson et al. (2007) implies a reduction in regional species richness as species shift their distributions to higher elevations. In mountain regions, the net effects of climate change on species richness will depend on the elevation where diversity peaks. Hence, in high latitude or high mountain environments, where diversity decreases with elevation, warming may lead to diversity increases (e.g., for alpine plants, Walther et al., 2005; Pauli et al., 2007). In contrast, diversity is likely to decrease with warming at low to mid-elevations and lower latitudes, including in highly diverse ecosystems such as the Mediterranean biome and tropical forests (e.g., Colwell et al., 2008). Documentation of current elevational gradients in diversity may therefore be key to predicting how the biodiversity of mountain regions will be affected by global change (e.g., see Fleishman et al., 2000).

The models presented here appear to describe accurately the diversity and composition of the butterfly fauna in the current system. However, it would be valuable to test the generality of the models by applying them to other mountain ranges in the Iberian peninsula or other Mediterranean regions (e.g., see Mac Nally et al., 2003). In the absence of direct measurements of temperature, rainfall and other climate variables from a wide range of sites in the region, applicability of our models to explore potential climate change effects would require transforming the surrogate variables (e.g. elevation) into climate variables using current estimated lapse rates in the area (Wilson et al., 2005). We are currently recording temperature and relative humidity from a subset of sample sites to confirm potential relationships of local climate with species abundance, distributions and diversity. Furthermore, models of future changes to species richness may need to include information on rates of range expansion and contraction related to habitat availability and processes such as metapopulation dynamics (Menéndez et al., 2006; Anderson et al., 2009).

CONCLUSIONS

Our results suggest that at a detailed geographical scale, topoclimatic rather than land-cover factors may be the main determinants of butterfly species diversity in a Mediterranean mountain region. Climate change, rather than direct changes to land use, is likely to be the key driver of recent changes to butterfly diversity in the study system; and the relationship of species richness with temperature and other climatic factors, influenced by elevation may lead to a predictable loss of butterfly diversity in mountain regions over coming decades.

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CAPÍTULO IV: Elevational trends in butterfly phenology: Implications for species responses to recent climate change.

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Cover photograph: View of the “Valle del Paular” from the transect “Mirador los Robledos”.

Photo: Javier Gutiérrez Illán

ABSTRACT

Recent climate change has led to widespread changes in animal and plant seasonality, leading to debate about its potential to cause phenological mismatches among interacting taxa. In mountainous regions, populations of many species show pronounced phenological gradients over short geographic distances, presenting the opportunity to test for possible limitations on activity periods related to regional climatic conditions. Here we show for 32 butterfly species sampled for 5 years in a 560-2260 m Mediterranean mountain range, that flight period shows more pronounced declines with elevation for species associated with lower elevations, and to some extent for species flying earlier in the season. Species restricted to high elevations and flying late in the season, many of which have shown range retractions associated with recent climate warming, show synchronised flight periods across their elevational ranges. We speculate as to the causes of this pattern, and the consequences for future responses to climate change.

Keywords

AICc, elevational range, GIS, GLM, Iberian Peninsula, Lepidoptera, phenology.

INTRODUCTION

Changes to the phenology of species represent one of the main ecological responses to recent climate change (Parmesan & Yohe 2003, Root et al 2004). Insect phenology may be particularly sensitive to the magnitude and rate of temperature change, because growth rates and emergence from winter diapause are directly linked to temperature in many insect species (Lawton, 1995; Bale et al., 2002). Changes to insect phenology may be important in influencing the wider ecological effects of climate change, since insects represent an important numerical fraction of global biodiversity and carry out key biotic interactions such as pollination and herbivory (e.g. see Bale et al., 2002; Memmott et al., 2007). However, multi-species datasets on insect phenology are rather limited (see Wilson et al. 2007a).

The Lepidoptera are the insect group with the most evidence for recent phenological changes linked to environmental conditions, largely because of the existence of several long-term databases (Roy & Sparks, 2000; Stefanescu et al. 2003; Forister & Shapiro 2003). Many such studies have focused on patterns in butterfly flight periods over time and over large geographic scales, often identifying a strong relationship between temperature and phenology (Shapiro, 1975; Dennis, 1993; Sparks & Yates, 1997; Roy & Asher, 2003). In mountainous regions with steep elevational gradients, temperature and hence insect phenology may change markedly over short geographic distances (Fielding et al., 1999; Körner, 2007). Therefore the responses of insect species to existing elevational climate gradients could be used to predict the effects of future climate change (Fielding et al., 1999), minimising the potentially confounding effects of photoperiod and different habitat types (Hill & Hodkinson, 1995; Butterfield, 1996; Fielding et al 1999). However, relatively little evidence exists for the effects of elevational gradients on the phenology of butterflies (but see Gutiérrez & Menéndez, 1998).

In general, insect flight occurs later in cooler years (Roy & Sparks, 2000; Stefanescu et al. 2003), at higher latitudes (Roy & Asher, 2003) and at higher elevations (Gutierrez & Menéndez, 1998; Merrill et al. 2008; Ashton et al. 2009). Thus, at a regional and local scale, a gradual delay in flight period is expected as latitude or elevation increase, and the upper latitudinal or elevational limits to species distributions may partly be set by temperature availability for development and adult activity (Thomas 1993; Crozier, 2004). Species which fly at high elevations or late in the year need to ensure that development, flight and breeding occur before the onset of unsuitable autumn weather. Therefore, such species may need to avoid the delays in emergence at increasing elevations which have been recorded for some insects (Gutiérrez and Menéndez 1998; Hodkinson 2005).

The present paper deals with patterns in the phenology of butterfly populations along an elevational gradient in an Iberian mountain range over five years. The main aims of the study are: (i) to examine the effects of elevation on mean flight-period date of butterfly populations, with the expectation that flight occurs later in the season as elevation increases, both among and within species; (ii) to detect inter-relationships between the rate at which phenology is delayed at increasing elevations ("elevational delays in phenology") and the elevational associations of the species; and (iii) to determine the relationships of elevational delays in phenology and mean flight-period date. Species flying at high elevations and/or late in the season are expected to present less elevational delay in their phenology, because of the increasing unpredictability of weather conditions in late summer and at higher elevations.

MATERIALS & METHODS

Study system

The study system includes 40 sites in and around the Sierra de Guadarrama in central Spain (approximately 41ºN 4ºW), encompassing plains with elevations of ≥500 m (to the south) and ≥700 m (to the north), and a mountain range which reaches a maximum elevation of 2430 m. (Fig. 1). Typical vegetation types are evergreen broadleaf woodland (largely *Quercus* *rotundifolia*) below 1000 m, deciduous woodland (largely *Quercus pyrenaica*) at roughly 1000-1500 m, and coniferous woodland (*Pinus sylvestris*) at approximately 1500-2000 m. Scrub and open grassland are present at all elevations, including beyond 2000 m (Rivas-Martínez *et al.*, 1987). Survey sites were open areas occurring in natural or semi-natural habitat (usually woodland clearings, scrub or pasture), selected based on accessibility and to provide a representative sample of all elevations in the region (Figs. 1 and 2). Nearest neighbouring sites were 4.13 ± 0.67 km apart (based on the full sample of 40 sites) such that for the species analysed, transects represent independent populations, where the measures of flight period depend much more strongly on local patterns of emergence than on immigrating individuals. On the first visit to each site, a 500 m transect route was established, passing through habitat typical of the location, and Universal Transverse Mercator (UTM) coordinates were recorded to the nearest metre at least every 100 m using a handheld Garmin GPS unit. Each transect route was plotted in ArcGIS 8.1 (ESRI, 2001), and a 100 m digital elevation model (NASA/JPL-Caltech 2004) was used to estimate its mean elevation, based on transect centroids estimated by the Spatial Analyst tool (ESRI, 1996).

Butterflies were sampled at 20 sites in 2004 and 2005 (elevation range 926-2050 m.), 34 sites in 2006, and 40 sites in 2007-08 (elevation range 560-2260 m in 2006-08) (Figs. 1 and 2). Standardized 500 m long x 5 m wide transects were walked at each site every two weeks during suitable conditions for butterfly activity (Pollard & Yates, 1993), from April/May to October in 2004-06, and from March to October in 2007-08, when recording began earlier to ensure that butterfly flight periods were recorded from initial emergence at the additional lower elevation sample sites.

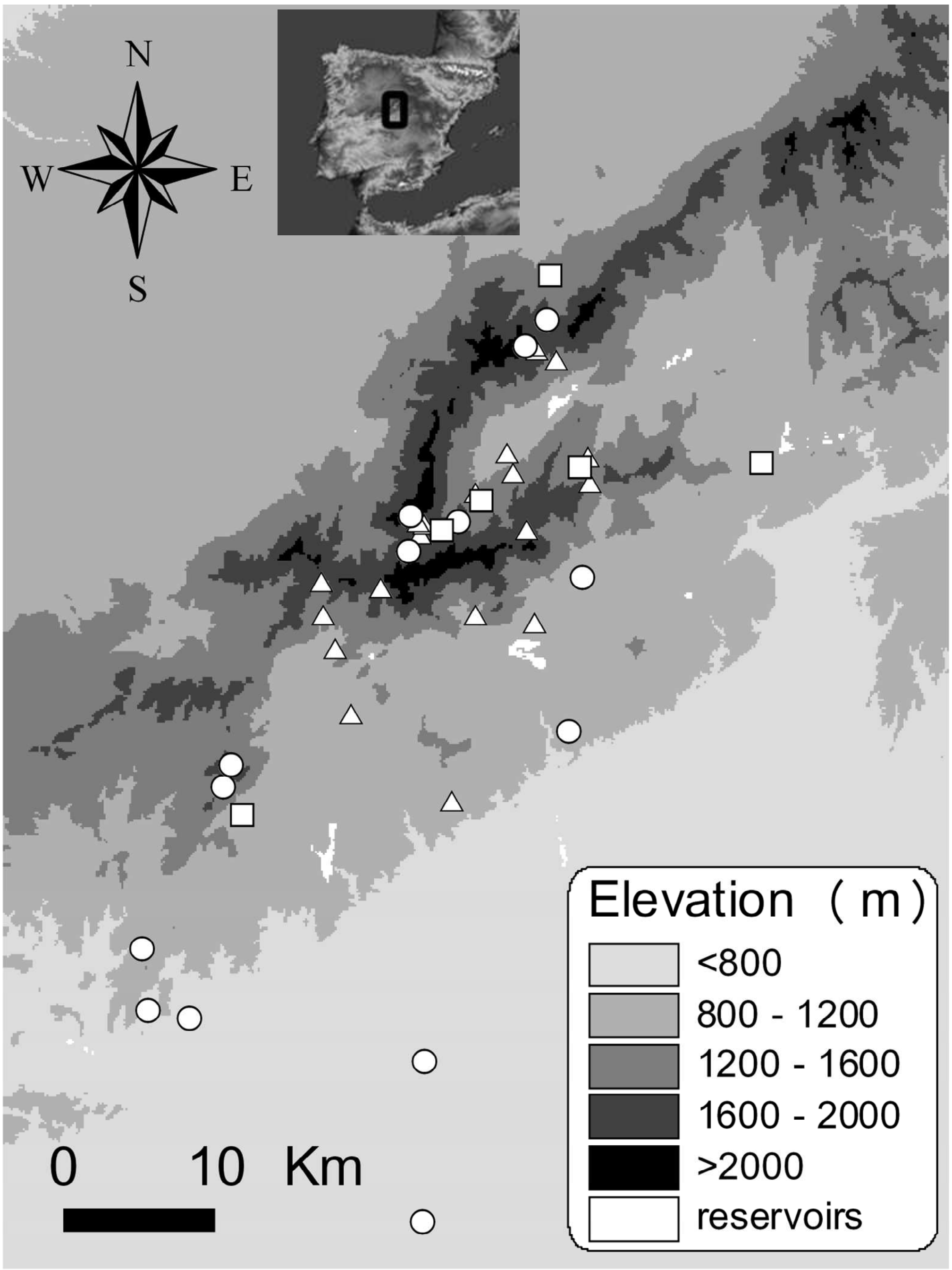

Figure 1 Map of the Sierra de Guadarrama showing elevation and 40 sample sites. Elevation is shown in 400 m bands from <800 m (pale grey) to >2000 m (black). Sample sites are triangles (20 sites sampled 2004-2008), circles (14 sites sampled 2006-2008) and squares (6 sites sampled in 2007 and 2008).

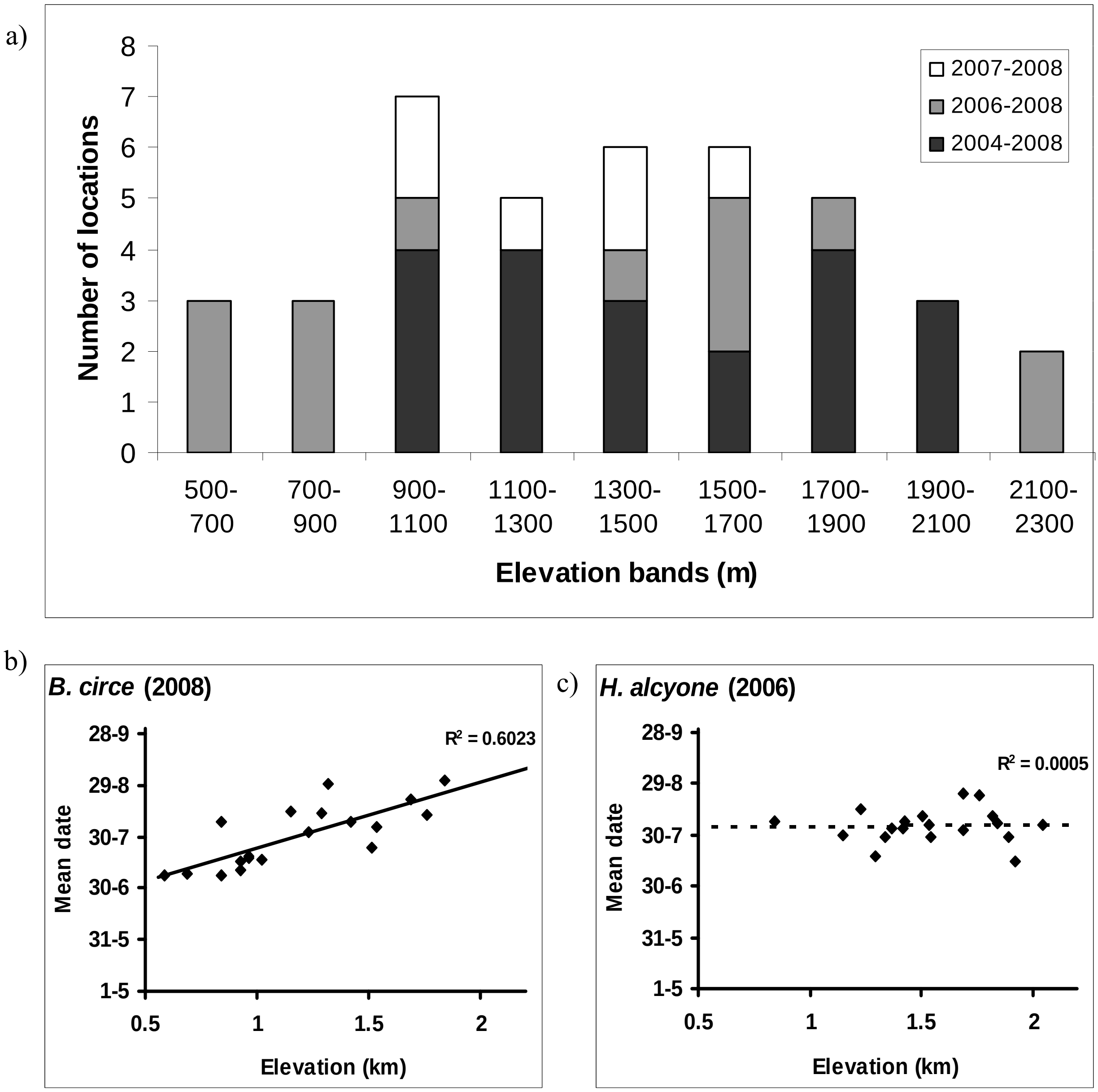

Figure 2 a) Histogram of sample sites at different elevations. Sites were sampled in 5 years (black), 3 years (grey) or 2 years (white). Panels b and c showing the elevation delay for two species included in the analyses: b) *Brintesia circe* in 2008 model (elevational delay = 38.56 days/km) and c) *Hipparchia alcyone* in 2006 model (elevational delay = 0.69 days/km).

Butterfly phenology and elevational associations

For each year, we analysed data for species with one annual generation (univoltine) for which two or more individuals were counted in at least five transect locations. In order to ensure that analyses include species whose phenology was representatively sampled, we exclude sites where only one individual was recorded. We also exclude (a) species from genera which could not be reliably identified in the field (e.g. *Mellicta spp*, *Pyrgus spp*), (b) tree-living species which are likely to be under-recorded by transects (e.g. *Thecla quercus*), (c) migratory species, and (d) species which present summer aestivation (e.g. *Maniola jurtina*, *Hipparchia semele*) (García-Barros, 1987, 1988).

The date of the annual flight period for each species (at each site with two or more individuals recorded) was summarised as the *Weighted mean flight date*. This statistic is widely used in studies of butterfly phenology (e.g. Roy & Sparks 2000, Stefanescu et al. 2003), and was calculated as *Weighted mean date* = (∑ *Number of butterflies per visit* x *Date*) / *Annual total number of butterflies*. Date was measured as the number of days elapsed since December 31st. Elevational delays in phenology were tested for by regressing mean flight date against the elevation of each transect site: the delay (days per km) was the slope of the regression (see Merrill et al., 2008) (Fig. 2). To determine whether elevational delays in phenology were consistently greater for some species than others, we carried out Spearman's rank correlations of elevational delay among species between pairs of years.

To investigate the relationship of phenological delay with distribution size, elevational associations, and flight period, we also calculated the following measures for each species and each year: prevalence (proportion of sample sites where the species was present); maximum elevation site where the species was recorded, minimum elevation site, mean elevation (average elevation of all sites where the species was recorded) and elevation range (difference between maximum and minimum elevation) (all in m); as well as the "global" weighted mean date of the flight period, including data from all sites where the species was recorded. The final set of variables and their values for each species and each year is listed in Table S1.

Data analyses

We then tested several hypotheses for the possible factors determining the elevational delay in phenology. The main hypotheses were i) later flying species have reduced delay, because of selection against late-season flying due to avoid unfavourable conditions, ii) species with higher elevational associations have reduced delay, because of selection against flying late in the season at the highest locations and iii) species with wider elevational range have larger delays, because it is statistically more probable to detect elevational delays when a given species flies in a larger number of sites and/or in a wider elevational range. To test these hypotheses we carried out linear regressions with annual elevational delay as response variable against global mean flight date and the elevational associations of each species. To test whether observed patterns were influenced by the number of populations included in analysis, elevational delay was also regressed against species prevalence. Phylogenetic relationships can influence results obtained from multi-species analyses (Harvey & Pagel, 1991). To control for phylogenetic non-independence, we used the freely available software package COMPARE (Martins 2004) to run phylogenetic generalized least squares (PGLS) regressions (Martins & Hansen 1997), with a butterfly phylogeny based on those presented in Harvey (1991), Cowley et al. (2001) and that recently used in Wilson et al. (2005) (Fig. S1).

To tease out whether global mean date, elevational associations and prevalence were all significant predictors of the magnitude of elevational delay in phenology, we generated generalized linear models for each year, using a forward AICc-based procedure until no removal of terms improved the model (Akaike, 1974; Johnson & Omland, 2004). AICc is a second order derivative of the Akaike information criterion which contains a bias correction term for small sample size relative to the number of estimated parameters, and should be used when the number of free parameters exceeds N/40 (where N is sample size), as in this case (Burham & Anderson, 2002; Johnson & Omland, 2004). We also performed non-parametric correlations for each year between the predictor variables, to control for possible inter-correlations. It was expected that both global mean date and the elevational associations of species would affect phenological delay in the same direction. In other words, late-flying species would also fly at high elevations (because of fewer growing day degrees at high elevations in spring and summer), and both late flight periods and high elevational associations would be associated with shallow elevational delays in phenology. Because of the possible correlation between the two variables, we performed regressions of global mean date against mean altitude for all species analysed per year, and then calculated the residuals as a measure of whether species fly relatively "early" in the season for their altitudinal associations (negative residuals), or relatively "late" in the season (positive residuals). We used the residuals from this regression as a predictor variable to test whether flight period affected elevational delay, independent of the elevational associations of species.

RESULTS

Field survey

Between 20 and 29 species satisfied the criteria for analysis in each year (Table 1), with 19 species satisfying the criteria in all five years and 32 species included in at least one year. The relative prevalence of the 19 species analysed in all years was strongly positively correlated between years ($r_s > 0.71$, $P < 0.001$, $n = 19$ in all cases).

Table 1 Summary for delays in phenology with elevation in each year. The last column shows the proportion of species that presented significant (p<0.05) elevational delay in phenology (days/km).

Year	N species	N locations	Mean delay (days/km) (±SE)		% of species with significant elevational delay
			All species	Species with significant delay (P<0.05)	
2004	20	20	15.59 ± 3.20	23.43 ± 2.14	40
2005	24	20	14.76 ± 2.87	25.02 ± 2.63	42
2006	29	34	22.16 ± 4.51	31.20 ± 4.18	41
2007	29	40	22.28 ± 2.79	29.44 ±2.83	55
2008	27	40	23.75 ± 3.38	34.48 ± 4.10	45

Data analyses

Univariate analyses

In all years 40-55% of species showed a significant elevational delay in phenology (Table 1). The average delay was estimated as 14-16 days per km in 2004-05 (when total elevation range was 926-2050 m) and 22-24 days per km in 2006-08 (elevation range 560-2260 m). The average estimated delay was larger when including only those species with significant relationships (Table 1). Although the species showing significant relationships were not completely consistent from year to year (with 23 out of the 32 species showing significant relationships in one or more years, Table 2), the elevational delay for the 19 species recorded in all years was positively correlated between years (all $r_s > 0.5$, $P < 0.05$, n=19). The elevational delay in phenology for the final list of species included in each year is shown in Table S2.

There was a consistent negative effect of global mean date on elevational delay in all years, which was significant ($P<0.05$) in 2004, 2007 and 2008 (Table 2). Earlier flying species tended to have longer delays with elevation (Fig. 3).

There was a very consistent negative effect of altitude in all years (Fig. 3), and all the elevational associations of species (max, min and mean) led to similar results. Species flying at lower altitudes had longer delays with elevation. Minimum and mean altitude were significant in all years (Table 2), and maximum altitude was significant in all years except 2004. Mean altitude explained the greatest proportion of variation in all years except 2004.

We found no effect of prevalence and altitudinal range of species for any year (Table 3). There was no clear effect of phylogeny, with PGLS analyses not varying the significance or direction of results based on ordinary least squares regressions, and very similar variable coefficients estimated from the PGLS analyses (results not shown).

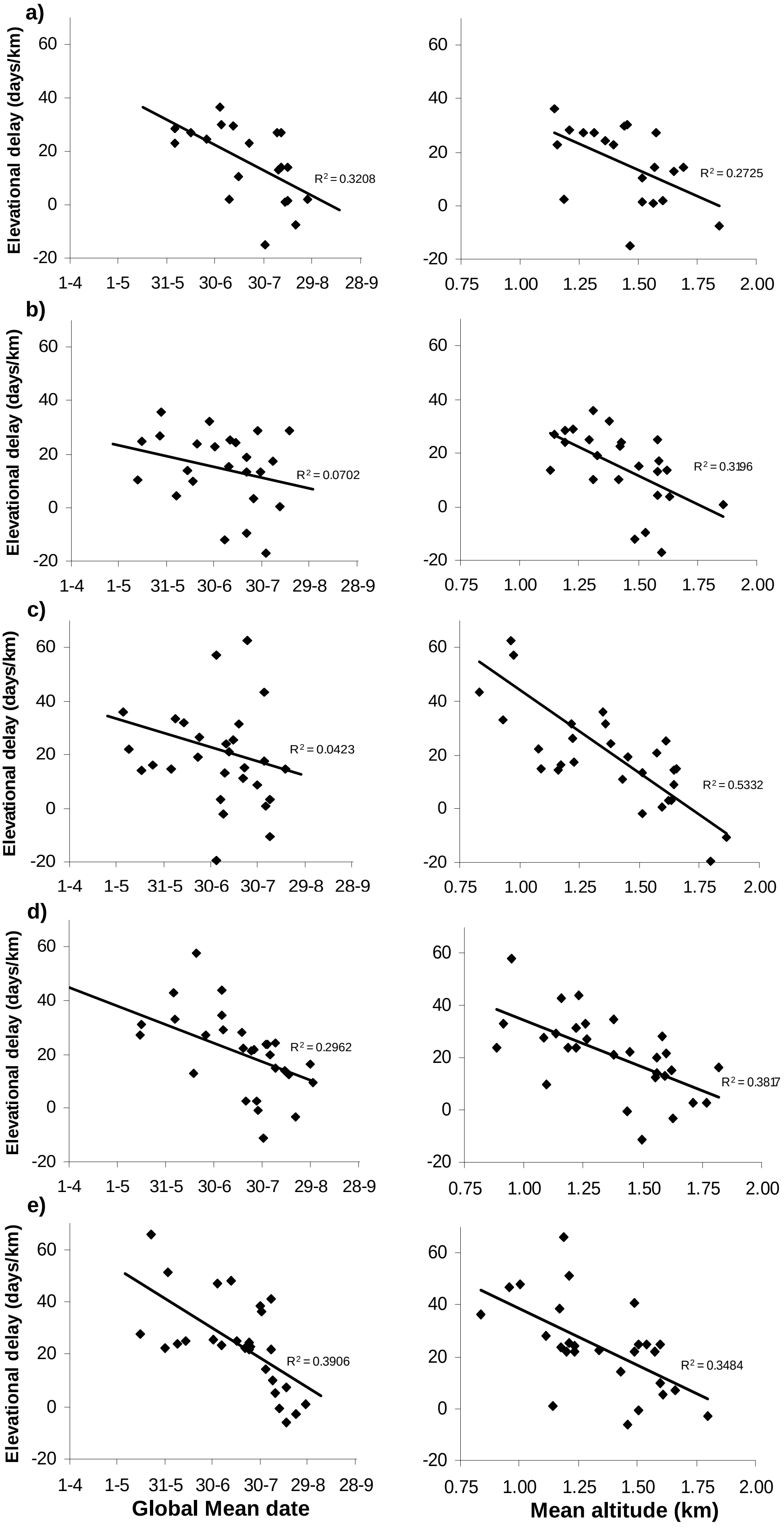

Figure 3 Linear regression of mean elevational delay in phenology against global mean date and mean elevation of the selected species in the five years of study: 2004 (a); 2005 (b); 2006 (c); 2007 (d) and 2008 (e).

Table 2 Summary for the results obtained in univariate analyses for the 32 species included in at least one year in the analyses.

Species	Years sampled	%Years with significant delay	Mean delay (±SE)	Average mean date	Average mean alt. (Km.)	Mean prevalence
Aporia crataegi	5	40	23.76 ± 3.65	22 Jun	1.32	0.44
Argynnis adippe	5	40	15.39 ± 3.41	29 Jul	1.61	0.44
Argynnis aglaja	5	80	20.53 ± 2.67	16 Jul	1.56	0.48
Argynnis niobe	5	80	28.22 ± 2.78	2 Jul	1.45	0.69
Argynnis paphia	5	20	3.24 ± 10.46	28 Jul	1.48	0.37
Coenonympha arcania	5	0	18.86 ± 5.4	12 Jul	1.46	0.33
Erebia triaria	5	20	16.76 ± 4.19	11 Jun	1.59	0.35
Euphydryas aurinia	5	40	33.18 ± 6.21	31 May	1.18	0.32
Hesperia comma	5	40	7.65 ± 3.7	12 Aug	1.62	0.57
Hipparchia alcyone	5	0	-1.45 ± 5.06	9 Aug	1.55	0.50
Hipparchia statilinus	5	0	11.27 ± 5.01	23 Aug	1.14	0.50
Hyponephele lycaon	5	20	6.91 ± 2.93	7 Aug	1.57	0.63
Kanetisa circe	5	80	28 ± 3.35	27 Jul	1.25	0.63
Lycaena alciphron	5	40	8.64 ± 7.3	11 Jul	1.57	0.49
Lycaena virgaureae	5	40	11.59 ± 2.2	1 Aug	1.64	0.48
Melanargia lachesis	5	100	23.02 ± 0.56	18 Jul	1.38	0.88
Melitaea cinxia	4	25	23.61 ± 3.84	1 Jun	1.20	0.19
Pyronia bathseba	5	40	37.67 ± 8.72	21 Jun	1.02	0.27
Pyronia tithonus	5	100	23.90 ± 1.96	4 Aug	1.22	0.52
Satyrus actaea	5	20	-0.87 ± 5.12	17 Aug	1.84	0.28
Glaucopsyche alexis	2	50	28.90 ± 6.83	29 May	1.27	0.26
Zerynthia rumina	4	50	25.56 ± 1.31	13 May	1.14	0.35
Thymelicus sylvestris	4	100	29.43 ± 4.93	28 Jun	1.21	0.46
Brenthis daphne	4	0	10.48 ± 3.73	19 Jul	1.47	0.25
Anthocharis cardamines	4	75	35.88 ± 11.49	14 May	1.27	0.38
Pyronia cecilia	3	67	40.95 ± 11.34	29 Jul	0.90	0.30
Erebia meolans	2	0	-8.26 ± 11.08	11 Jul	1.75	0.19
Hyponephele lupinus	1	0	43.50	3 Aug	0.83	0.18
Laeosopis roboris	1	0	108.29	19 Jun	0.94	0.15
Thymelicus acteon	3	100	44.79 ± 8.27	7 Jul	1.04	0.18
Tomares ballus	1	0	33.09	23 Mar	0.92	0.23
Melanargia russiae	1	0	2.56	27 Jul	1.77	0.18

Table 3 Summary of the results obtained for each year in linear regressions of elevational delay in phenology against selected variables. Results were consistent with those obtained using PGLS in COMPARE software.

Year		Prevalence	Global mean date	Max alt	Min alt	Mean alt	Alt range
2004	R^2	0.02	0.32	0.12	0.35	0.27	0.02
	F	0.42	8.50	2.45	9.58	6.74	0.44
	p-value	0.53	<0.01	0.14	<0.01	<0.01	0.52
	Slope	10.89	-0.32	-24.04	-48.89	-38.86	11.25
2005	R^2	0.02	0.07	0.25	0.24	0.32	0.03
	F	0.40	1.66	7.44	6.95	10.33	0.76
	p-value	0.53	0.21	0.01	0.01	<0.01	0.39
	Slope	10.50	-0.13	-32.13	-44.20	-42.90	-13.68
2006	R^2	0.07	0.04	0.41	0.45	0.53	<0.01
	F	2.09	1.19	18.43	22.37	30.84	0.05
	p-value	0.16	0.28	<0.01	<0.01	<0.01	0.83
	Slope	-34.46	-0.18	-49.01	-58.10	-62.07	-3.48
2007	R^2	0.01	0.30	0.30	0.36	0.38	0.02
	F	0.17	11.36	11.28	15.29	16.67	0.41
	p-value	0.68	<0.01	<0.01	<0.01	<0.01	0.53
	Slope	7.09	-0.23	-31.36	-31.24	-35.83	6.83
2008	R^2	0.06	0.39	0.32	0.14	0.35	0.09
	F	1.49	16.02	11.96	3.92	13.37	2.39
	p-value	0.23	<0.01	<0.01	0.05	<0.01	0.14
	Slope	-28.04	-0.37	-32.29	-24.68	-43.37	-19.27

Multivariate models

All variables describing elevational associations were strongly correlated to each other in all years (Table S3). To avoid problems derived from multicollinearity of predictor variables, we excluded maximum and minimum elevation from stepwise modelling, including mean elevation only based on its stronger relationships with elevational delay in the univariate models. The results from the stepwise GLMs for elevational delay in phenology were very similar to those obtained from univariate analyses (Table 4). Mean altitude was selected with a negative effect in all years. We also found a negative effect of global mean date in the models for 2004, 2007 and 2008. Prevalence was selected as an additional third variable in 2004, showing a positive relationship with elevational delay (i.e. species occupying a higher proportion of sample locations had a greater delay with elevation). Because global mean date was significantly correlated with mean altitude in 2005, 2007 and 2008, we performed the modelling using the residuals of the regression between global mean date against mean elevation as the measure of overall flight period. Using the residuals instead of global mean date did not lead to any differences in the direction or significance of our results (Table 3).

Table 4 Coefficients of variables selected in the stepwise GLMs for the five years of study.

	Sample size (species)	Coefficients (±SE)		
		Prevalence	Global mean date*	Mean alt
2004	20	25.24 (±11.87)	-0.32 (±0.10)	-22.66 (±11.54)
2005	24			-42.90 (±12.78)
2006	29			-62.07 (±10.79)
2007	29		-0.13 (±0.06)	-26.60 (±9.37)
2008	27		-0.28 (±0.08)	-29.72 (±10.61)

DISCUSSION

In the present study, we examined the effects of elevational gradients on the phenology of butterfly populations in a highly mountainous region. Based on information for five years, we found that the flight periods of populations of individual species tend to occur later at higher elevations, but that the elevational delay in phenology was not consistent among species or years. Instead, species associated with higher elevations and those flying later in the year tend to have more synchronised emergence across their elevational range than species flying in spring or early summer.

Several studies have focused on the effects of temperature on the phenology of butterflies (Roy and Sparks, 2000; Stefanescu et al., 2003; Menzel et al., 2006), since the appearance and flight dates of these insects have become one of the most important tools for evaluating the effect of climate change on biodiversity. Although temperature has been demonstrated to be an important factor determining the phenology of butterflies (Parmesan & Yohe, 2003; Menzel et al, 2006), there are a large number of confounding factor such as land-use change which will surely affect the impact of climate change on the Lepidoptera fauna. On the other hand, the use of altitude as an indirect measurement of thermal associations has been argued to be an efficient method when there are no direct data on temperature (Körner, 2007), and the temperature / elevation lapse-rate has been used in several studies as a determinant of insect phenology (Gutiérrez & Menéndez, 1998; Fielding et al., 1999; Gutiérrez Illán et al., *in press*).

According to current knowledge, advances in the timing of butterflies are expected as temperature increases (Roy & Sparks, 2000; Stefanescu et al., 2003). Our work indicates that the phenology of the species with significant elevational delays was delayed from 23 to 34 days per km in the five years of study. According to the regional lapse-rate (6ºC per 1000 m elevational increase) reported by Wilson et al., 2005, our results suggest that a 1ºC rise in temperature could advance butterflies phenology by 3-6 days in the region. This trend is broadly in accordance with those obtained by Roy & Sparks, 2000 who reported an ascent of 1ºC implying an advance of 2-10 days in average flight date for British butterflies. Our results also support the findings of Gutiérrez & Menéndez, 1998, suggesting the tendency for timing to be later at higher and cooler altitudes.

It appears that both elevational associations and life cycle seasonality are important determinants of the elevational delays in phenology of butterflies in this mountain region. Linear regressions revealed a significant negative relationship between delays in phenology and the mean elevation of a species range in all years, suggesting that species flying at higher elevations have reduced delay, perhaps because of selection against flying either very early or very late in the season. With regards to relationships with phenological delay, results of overall mean flight date (including information from across the elevation range of each species) differed somewhat from those obtained with mean elevation. Multivariate stepwise modelling led to very similar results than those obtained in univariate analyses, revealing mean elevation and global flight date as the most important factors. Mean elevation was selected in all years and global flight date was selected as a second variable in all years where it was previously selected in univariate analyses (2004, 2007 and 2008). The most plausible explanation is a complementary effect of both variables in the same direction.

We found that species flying later in the season show less phenological delay with elevation. However, it is worth noting that, although we found a negative relationship of elevational delay with mean flight date in all years, it was not significant for 2005 and 2006, suggesting that climatic differences between years may influence the extent to which the regional flight periods of species are synchronised across elevations. This could be partially explained by the fact that in these years the appearance and peak dates of the majority of species were particularly early in the season, related to warm springs (unpublished data), which might lead to a synchronisation of flight periods across elevations for early flying species. A further possibility is that the general relationship between delay and global mean flight date reflects a shorter longevity of adult butterflies flying towards the end of the summer, because of the onset of unfavourable conditions, or a lack of nectar sources in late summer. Such an explanation could help to explain why late flying species showed a reduced delay in 2005 and 2006, when overall phenology was earlier.

The number of species that presented elevational delays in phenology was similar in all years. However, we have found discrepancies between the species showing significant relationships in phenological delay with elevation from year to year, indicating that inter-year climate differences could affect the phenology patterns of those populations. We found that flight dates of low-elevation species and species that fly earlier in the season show pronounced delays in phenology as elevation incraeses while phenology of species that fly at high altitudes or late summer did not change with elevation. These results suggest that high elevation or late flying species may show local adaptations of populations to avoid unfavourable weather conditions at the end of summer and at high elevations. As discussed by Roy & Asher, 2003, synchrony in appearance across temperature gradients may provide evidence for local adaptations of butterfly populations to regional climates. Such adaptations could include behavioural and physiological processes, like selection of warm microhabitats for egg-laying at high elevations, or life history adaptations to larval growth rate or adult body size (Gotthard, 2004). There are some adaptations present in the literature that can be developed in the cooler locations of a species' range, like positive phototaxy and thermal adaptations of larvae, basking to achieve body temperatures 5-20ºC above ambient temperatures (Weiss et al., 1988), the ability to exploit warm microclimates (Thomas 1993), or reduced sizes of adults and larvae (Ayres & Scriber, 1994). These adaptations may result in the synchronised emergence between populations of a given species in different parts of its elevational range.

We did not find any effects of elevational range on delays in phenology suggesting that a wider elevational range does not reduce opportunities for local adaptations. Prevalence also had no clear effect on phenological delays, and in fact showed a significant positive relationship with elevational delay in 2004: this pattern contrasts with the possible hypothesis that high density populations and dispersal can synchronise phenology. Instead, the positive relationship with prevalence in 2004 may partly result from species with a greater number of populations having a better resolution of data to identify phenological patterns. No such relationship was seen in later years, when more sample sites and species were included in analyses.

The work implies that species that are able to adjust their phenology in this way might be able to adapt to changing climates. However, the adaptations could prove maladaptive under future climate conditions, if they are based on proxies of climate or microclimate, such as day length or microhabitat structure, rather than directly based on microclimatic conditions. Hence, locally adapted species may be unable to cope with the rapid forecasts of climate warming. Recent research suggests that plant species which do not advance their phenology with increasing temperatures have suffered declines in abundance compared with species where phenology has advanced (Willis et al. 2008). The high elevation and late-flying species in our study tend to be those which have also suffered range retractions at their low elevation limits associated with recent climate warming (Wilson et al. 2005), but it appears that overall elevational range is more closely related than phenological patterns to these declines. Nevertheless, the apparent associations between phenological synchronisation and elevational range imply that phenology models may be relevant for population responses to climate change, at least in mountainous landscapes. Evaluation of the role of phenology in influencing biotic interactions (e.g. Memmott et al. 2007) and microhabitat associations (e.g. Roy and

Thomas 2003; Wilson et al. 2007a) may be crucial to assess the importance of phenological change for species' ability to adapt or shift their distributions in response to climate change.

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SUPPLEMENTARY MATERIAL

Additional supporting information may be found in the supplementary section of this article: Table S1, S2, S3. Figure S1

Table S1 Prevalence (proportion of sites occupied), global mean flight date and elevational associations (km) of selected species.

a) species 2004

	Prevalence	Global mean date	Max alt	min alt	mean alt	Alt range
Aporia crataegi	0.50	24/06/2004	1.84	0.93	1.36	0.91
Argynnis adippe	0.55	08/08/2004	2.05	1.05	1.65	1.00
Argynnis aglaja	0.45	14/07/2004	1.99	1.15	1.52	0.84
Argynnis niobe	0.75	03/07/2004	2.05	0.93	1.46	1.12
Argynnis paphia	0.30	30/07/2004	1.84	1.23	1.46	0.61
Coenonympha arcania	0.30	11/07/2004	1.84	1.15	1.44	0.69
Erebia triaria	0.40	15/06/2004	1.92	1.23	1.58	0.69
Euphydryas aurinia	0.45	05/06/2004	1.54	0.93	1.21	0.61
Hesperia comma	0.80	13/08/2004	2.05	1.05	1.57	1.00
Hipparchia alcyone	0.40	13/08/2004	1.89	1.23	1.52	0.66
Hipparchia statilinus	0.55	26/08/2004	1.51	0.93	1.19	0.58
Hyponephele lycaon	0.80	12/08/2004	2.05	0.93	1.56	1.12
Kanetisa circe	0.75	07/08/2004	1.84	0.93	1.31	0.91
Lycaena alciphron	0.40	09/07/2004	1.99	1.29	1.61	0.70
Lycaena virgaureae	0.50	09/08/2004	2.05	1.23	1.69	0.82
Melanargia lachesis	0.90	21/07/2004	1.92	0.93	1.39	0.99
Melitaea cinxia	0.30	05/06/2004	1.51	0.93	1.16	0.58
Pyronia bathseba	0.25	02/07/2004	1.42	0.93	1.15	0.49
Pyronia tithonus	0.65	09/08/2004	1.78	0.93	1.27	0.85
Satyrus actaza	0.30	18/08/2004	2.05	1.51	1.84	0.54

b) species 2005

	Prevalence	Global mean date	Max alt	min alt	mean alt	alt range
Aporia crataegi	0.55	16/06/2005	1.89	0.93	1.42	0.96
Argynnis adippe	0.55	20/07/2005	2.05	1.05	1.62	1.00
Argynnis aglaja	0.70	10/07/2005	2.05	1.15	1.58	0.90
Argynnis niobe	0.75	26/06/2005	1.99	0.93	1.38	1.06
Argynnis paphia	0.55	20/07/2005	1.89	1.05	1.53	0.84
Coenonympha arcania	0.35	30/06/2005	1.84	1.15	1.42	0.69
Erebia triaria	0.40	05/06/2005	2.05	1.23	1.58	0.82
Euphydryas aurinia	0.30	26/05/2005	1.37	0.93	1.15	0.44
Hesperia comma	0.65	06/08/2005	2.05	1.05	1.59	1.00
Hipparchia alcyone	0.55	01/08/2005	2.05	1.15	1.60	0.90
Hipparchia statilinus	0.50	16/08/2005	1.54	0.93	1.19	0.61
Hyponephele lycaon	0.70	29/07/2005	2.05	1.15	1.58	0.90
Kanetisa circe	0.70	20/07/2005	1.89	0.93	1.33	0.96
Lycaena alciphron	0.45	06/07/2005	1.99	1.05	1.49	0.94
Lycaena virgaureae	0.50	25/07/2005	2.05	1.23	1.63	0.82
Melanargia lachesis	0.95	13/07/2005	2.05	0.93	1.43	1.12
Glaucopsyche alexis	0.35	27/05/2005	1.54	0.93	1.31	0.61
Pyronia bathseba	0.20	13/06/2005	1.54	0.93	1.13	0.61
Pyronia tithonus	0.60	27/07/2005	1.54	0.93	1.23	0.61
Satyrus actaea	0.25	10/08/2005	2.05	1.54	1.86	0.51
Zerynthia rumina	0.35	15/05/2005	1.84	0.93	1.29	0.91
Tymelicus sylvestris	0.45	19/06/2005	1.54	0.93	1.19	0.61
Brentis daphne	0.35	09/07/2005	1.89	1.23	1.50	0.66
Antocharis cardamines	0.40	12/05/2005	1.89	0.93	1.31	0.96

c) species 2006

	Prevalence	Global mean date	Max alt	min alt	mean alt	alt range
Aporia crataegi	0.47	13/06/2006	1.84	0.84	1.36	1.00
Argynnis adippe	0.41	14/07/2006	2.05	1.05	1.61	1.00
Argynnis aglaja	0.53	11/07/2006	2.15	1.02	1.57	1.13
Argynnis niobe	0.88	21/06/2006	2.26	0.69	1.45	1.57
Argynnis paphia	0.41	20/07/2006	1.89	1.02	1.43	0.87
Coenonympha arcania	0.29	08/07/2006	1.89	1.15	1.51	0.74
Erebia triaria	0.29	04/06/2006	2.05	1.23	1.64	0.82
Euphydryas aurinia	0.24	23/05/2006	1.43	0.93	1.17	0.50
Hesperia comma	0.56	06/08/2006	2.26	0.93	1.63	1.33
Hipparchia alcyone	0.56	04/08/2006	2.05	0.84	1.59	1.21
Hipparchia statilinus	0.44	17/08/2006	1.69	0.56	1.09	1.13
Hyponephele lycaon	0.56	29/07/2006	2.26	1.15	1.64	1.11
Kanetisa circe	0.62	17/07/2006	2.15	0.56	1.22	1.59
Lycaena alciphron	0.62	05/07/2006	2.26	1.05	1.62	1.21
Lycaena virgaureae	0.50	21/07/2006	2.05	1.23	1.66	0.82
Melanargia lachesis	0.82	09/07/2006	2.26	0.56	1.38	1.70
Melitaea cinxia	0.15	17/05/2006	1.69	0.93	1.16	0.76
Pyronia cecilia	0.32	23/07/2006	1.53	0.56	0.96	0.97
Pyronia bathseba	0.32	07/06/2006	1.51	0.56	0.93	0.95
Pyronia tithonus	0.41	03/08/2006	1.69	0.74	1.23	0.95
Satyrus actaea	0.32	07/08/2006	2.26	1.51	1.87	0.75
Antocharis cardamines	0.24	05/05/2006	1.99	0.84	1.35	1.15
Brentis daphne	0.29	09/07/2006	2.15	1.02	1.51	1.13
Erebia meolans	0.21	03/07/2006	2.05	1.43	1.80	0.62
Hyponephele lupinus	0.18	03/08/2006	1.34	0.56	0.83	0.78
Laeosopis roboris	0.15	19/06/2006	1.23	0.56	0.94	0.67
Zeryntia rumina	0.38	09/05/2006	1.51	0.56	1.08	0.95
Tymelicus sylvestris	0.50	23/06/2006	1.84	0.74	1.22	1.10
Tymelicus acteon	0.18	03/07/2006	1.51	0.56	0.98	0.95

d) species 2007

	Prevalence	Global mean date	Max alt	min alt	mean alt	alt range
Aporia crataegi	0.35	25/06/2007	1.69	0.93	1.26	0.76
Argynnis adippe	0.35	04/08/2007	2.05	1.05	1.56	1.00
Argynnis aglaja	0.40	24/07/2007	2.15	1.15	1.60	1.00
Argynnis niobe	0.70	04/07/2007	2.05	0.69	1.38	1.36
Argynnis paphia	0.35	31/07/2007	1.89	1.05	1.50	0.84
Coenonympha arcania	0.35	18/07/2007	1.89	1.02	1.45	0.87
Erebia triaria	0.35	17/06/2007	2.05	1.23	1.59	0.82
Euphydryas aurinia	0.33	05/06/2007	1.52	0.74	1.16	0.78
Hesperia comma	0.48	20/08/2007	2.15	1.02	1.62	1.13
Hipparchia alcyone	0.50	13/08/2007	2.15	1.05	1.56	1.10
Hipparchia statilinus	0.50	30/08/2007	1.92	0.59	1.09	1.33
Hyponephele lycaon	0.58	15/08/2007	2.15	0.93	1.55	1.22
Kanetisa circe	0.60	01/08/2007	2.15	0.56	1.22	1.59
Lycaena alciphron	0.50	17/07/2007	2.26	0.97	1.58	1.29
Lycaena virgaureae	0.43	07/08/2007	2.05	1.23	1.62	0.82
Melanargia lachesis	0.93	23/07/2007	2.26	0.59	1.38	1.67
Melitaea cinxia	0.18	06/06/2007	1.53	0.96	1.26	0.57
Pyronia bathseba	0.33	19/06/2007	1.42	0.56	0.95	0.86
Pyronia tithonus	0.50	07/08/2007	1.82	0.69	1.19	1.13
Satyrus actaea	0.28	29/08/2007	2.15	1.42	1.82	0.73
Antocharis cardamines	0.43	16/05/2007	1.69	0.59	1.22	1.10
Brentis Daphne	0.20	27/07/2007	1.84	1.15	1.43	0.69
Erebia meolans	0.18	20/07/2007	2.05	1.37	1.71	0.68
Tomares ballus	0.23	23/03/2007	1.51	0.56	0.92	0.95
Melanargia russiae	0.18	27/07/2007	2.15	1.42	1.77	0.73
Zerynthia rumina	0.40	15/05/2007	1.51	0.56	1.09	0.95
Tymelicus sylvestris	0.45	04/07/2007	1.84	0.69	1.23	1.15
Tymelicus acteon	0.23	05/07/2007	1.69	0.56	1.14	1.13
Pyronia cecilia	0.25	02/08/2007	1.53	0.56	0.89	0.97

e) species 2008

	Prevalence	Global mean date	Max alt	min alt	mean alt	alt range
Aporia crataegi	0.33	30/06/2008	1.51	0.74	1.21	0.77
Argynnis adippe	0.33	08/08/2008	2.26	1.05	1.61	1.21
Argynnis aglaja	0.33	23/07/2008	2.05	1.05	1.50	1.00
Argynnis niobe	0.38	15/07/2008	2.05	0.96	1.59	1.09
Argynnis paphia	0.25	06/08/2008	1.89	1.23	1.49	0.66
Coenonympha arcania	0.38	23/07/2008	1.89	1.15	1.49	0.74
Erebia triaria	0.33	13/06/2008	2.05	1.15	1.54	0.90
Euphydryas aurinia	0.30	02/06/2008	1.51	0.93	1.21	0.58
Hesperia comma	0.38	16/08/2008	2.26	1.23	1.66	1.03
Hipparchia alcyone	0.50	15/08/2008	1.92	0.74	1.46	1.18
Hipparchia statilinus	0.50	27/08/2008	1.92	0.56	1.14	1.36
Hyponephele lycaon	0.53	11/08/2008	2.05	0.84	1.50	1.21
Kanetisa circe	0.48	30/07/2008	1.84	0.59	1.17	1.25
Lycaena alciphron	0.50	20/07/2008	2.26	1.05	1.57	1.21
Lycaena virgaureae	0.48	06/08/2008	2.05	1.05	1.60	1.00
Melanargia lachesis	0.83	23/07/2008	2.05	0.59	1.34	1.46
Melitaea cinxia	0.15	08/06/2008	1.51	1.02	1.24	0.49
Pyronia bathseba	0.25	02/07/2008	1.42	0.56	0.96	0.86
Pyronia tithonus	0.43	06/08/2008	1.54	0.74	1.20	0.80
Satyrus actaea	0.28	22/08/2008	2.26	1.32	1.80	0.94
Antocharis cardamines	0.45	22/05/2008	1.69	0.59	1.19	1.10
Brentis daphne	0.15	02/08/2008	1.69	1.27	1.43	0.42
Glaucopsiche alexis	0.18	31/05/2008	1.69	0.84	1.24	0.85
Zerynthia rumina	0.28	15/05/2008	1.51	0.56	1.11	0.95
Tymelicus sylvestris	0.45	06/07/2008	1.69	0.59	1.18	1.10
Tymelicus acteon	0.13	12/07/2008	1.51	0.56	1.00	0.95
Pyronia cecilia	0.33	31/07/2008	1.05	0.56	0.84	0.49

Table S2 Results of linear regressions of mean flight date against elevation for each species and each year.

a) species 2004

	R^2	F	p-value	Intercept (days after 1 Jan)	Elevational delay (days/km)
Aporia crataegi	0.60	12.1	0.008	143	24.5
Argynnis adippe	0.12	1.3	0.293	199	12.9
Argynnis aglaja	0.18	1.6	0.250	180	10.4
Argynnis niobe	0.79	47.9	<0.001	142	30.0
Argynnis paphia	0.11	0.5	0.515	234	-15.1
Coenonympha arcania	0.57	5.3	0.083	151	29.5
Erebia triaria	0.53	6.8	0.040	124	27.2
Euphydryas aurinia	0.41	4.9	0.061	123	28.4
Hesperia comma	0.31	6.3	0.025	204	14.2
Hipparchia alcyone	0.00	<0.1	0.940	224	1.4
Hipparchia statilinus	0.01	<0.1	0.813	236	2.2
Hyponephele lycaon	0.00	<0.1	0.833	223	0.9
Kanetisa circe	0.33	6.4	0.025	184	27.2
Lycaena alciphron	0.01	<0.1	0.857	188	1.8
Lycaena virgaureae	0.41	5.7	0.045	198	14.2
Melanargia lachesis	0.67	32.5	<0.001	171	23.0
Melitaea cinxia	0.48	3.6	0.129	130	23.0
Pyronia bathseba	0.43	2.3	0.227	142	36.4
Pyronia tithonus	0.41	7.6	0.019	188	27.1
Satyrus actaea	0.14	0.7	0.459	245	-7.5

b) species 2005

	R^2	F	p-value	Intercept (days after 1 Jan)	Elevational delay (days/km)
Aporia crataegi	0.21	2.3	0.165	153	10.04
Argynnis adippe	0.18	1.9	0.200	179	13.47
Argynnis aglaja	0.58	16.4	0.002	150	25.18
Argynnis niobe	0.74	36.2	<0.001	131	32.17
Argynnis paphia	0.19	2.1	0.184	215	-9.6
Coenonympha arcania	0.53	5.7	0.060	148	22.68
Erebia triaria	0.03	0.2	0.685	149	4.2
Euphydryas aurinia	0.34	2.1	0.220	114	26.85
Hesperia comma	0.44	8.8	0.013	189	17.15
Hipparchia alcyone	0.17	1.8	0.220	240	-16.94
Hipparchia statilinus	0.24	2.4	0.160	194	28.63
Hyponephele lycaon	0.37	6.9	0.022	188	13.08
Kanetisa circe	0.27	4.4	0.059	176	18.89
Lycaena alciphron	0.3	3.0	0.128	205	-12.06
Lycaena virgaureae	0.04	0.4	0.572	199	3.59
Melanargia lachesis	0.89	132.8	<0.001	159	24.05
Glaucopsyche alexis	0.7	11.6	0.020	101	35.72
Pyronia bathseba	0.15	0.3	0.617	149	13.67
Pyronia tithonus	0.56	13.0	0.005	172	28.82
Satyrus actaea	<0.01	<0.001	0.997	221	0.57
Zerynthia rumina	0.24	1.6	0.265	103	24.88
Tymelicus sylvestris	0.48	6.5	0.038	141	23.96
Brentis daphne	0.45	4.2	0.097	167	15.17
Antocharis cardamines	0.18	1.3	0.295	118	10.13

c) species 2006

	R^2	F	p-value	Intercept (days after 1 Jan)	Elevational delay (days/km)
Aporia crataegi	0.59	20.34	<0.001	120	31.79
Argynnis adippe	0.55	14.58	0.002	155	25.32
Argynnis aglaja	0.38	9.92	0.006	158	20.85
Argynnis niobe	0.54	33.31	<0.001	144	19.16
Argynnis paphia	0.09	1.1	0.316	184	11.14
Coenonympha arcania	<0.01	0.02	0.887	192	-1.99
Erebia triaria	0.08	0.7	0.428	131	14.57
Euphydryas aurinia	0.19	1.38	0.284	124	16.29
Hesperia comma	0.04	0.61	0.447	213	3.08
Hipparchia alcyone	<0.01	0.01	0.930	214	0.69
Hipparchia statilinus	0.18	2.78	0.120	213	14.7
Hyponephele lycaon	0.12	2.33	0.145	195	8.86
Kanetisa circe	0.39	12.14	0.002	163	31.49
Lycaena alciphron	<0.01	0.13	0.721	181	3.16
Lycaena virgaureae	0.17	3.11	0.098	177	14.99
Melanargia lachesis	0.88	180.29	<0.001	158	24.2
Melitaea cinxia	0.44	2.26	0.230	120	14.34
Pyronia cecilia	0.83	41.37	<0.001	149	62.45
Pyronia bathseba	0.33	4.44	0.064	129	33.31
Pyronia tithonus	0.33	5.85	0.032	194	17.48
Satyrus actaea	0.18	1.92	0.199	238	-10.56
Antocharis cardamines	0.89	46.46	<0.001	80	36.12
Brentis daphne	0.16	1.51	0.253	170	13.35
Erebia meolans	0.2	1.27	0.311	219	-19.33
Hyponephele lupinus	0.52	4.3	0.107	183	43.5
Laeosopis roboris	0.74	8.34	0.063	57	108.29
Zeryntia rumina	0.63	18.96	0.001	104	22.13
Tymelicus sylvestris	0.55	18.52	0.001	141	26.25
Tymelicus acteon	0.8	15.47	0.017	120	57.11

d) species 2007

	R^2	F	p-value	Intercept (days after 1 Jan)	Elevational delay (days/km)
Aporia crataegi	0.23	3.66	0.080	141	27.1
Argynnis adippe	0.36	6.71	0.024	184	19.98
Argynnis aglaja	0.35	7.58	0.016	172	21.58
Argynnis niobe	0.75	78.26	<0.001	136	34.81
Argynnis paphia	0.11	1.49	0.246	227	-11.12
Coenonympha arcania	0.17	2.5	0.140	167	22.39
Erebia triaria	0.13	1.73	0.213	147	12.99
Euphydryas aurinia	0.7	25.25	<0.001	103	43.13
Hesperia comma	0.01	0.17	0.684	237	-3.26
Hipparchia alcyone	0.09	1.76	0.201	203	13.91
Hipparchia statilinus	0.12	2.41	0.138	231	9.7
Hyponephele lycaon	0.15	3.83	0.064	207	12.63
Kanetisa circe	0.37	12.88	0.002	185	23.89
Lycaena alciphron	0.33	8.94	0.008	152	28.05
Lycaena virgaureae	0.24	4.7	0.047	194	15.11
Melanargia lachesis	0.74	98.44	<0.001	174	21.09
Melitaea cinxia	0.62	8.28	0.035	114	33.12
Pyronia bathseba	0.72	28.38	<0.001	115	57.94
Pyronia tithonus	0.57	23.54	<0.001	189	24.07
Satyrus actaea	0.45	7.39	0.024	211	16.26
Antocharis cardamines	0.26	5.35	0.035	97	31.39
Brentis Daphne	<0.01	0.01	0.924	208	-0.66
Erebia meolans	0.03	0.13	0.730	195	2.82
Tomares ballus	0.3	3.06	0.124	55	33.09
Melanargia russiae	<0.01	0.02	0.887	202	2.56
Zerynthia rumina	0.42	10.06	0.007	103	27.44
Tymelicus sylvestris	0.6	24.1	<0.001	131	44.11
Tymelicus acteon	0.59	9.92	0.016	155	29.08
Pyronia cecilia	0.13	1.2	0.304	193	23.96

e) species 2008

	R^2	F	p-value	Intercept (days after 1 Jan)	Elevational delay (days/km)
Aporia crataegi	0.15	1.88	0.198	150	25.36
Argynnis adippe	0.04	0.48	0.502	212	5.27
Argynnis aglaja	0.33	5.36	0.041	167	24.64
Argynnis niobe	0.24	4.14	0.063	156	24.96
Argynnis paphia	0.52	8.62	0.019	160	40.9
Coenonympha arcania	0.26	4.64	0.051	172	21.73
Erebia triaria	0.29	4.44	0.059	126	24.86
Euphydryas aurinia	0.44	7.9	0.018	93	51.21
Hesperia comma	0.14	2.17	0.164	216	7.08
Hipparchia alcyone	0.03	0.48	0.498	237	-6.31
Hipparchia statilinus	<0.01	0.008	0.928	238	1.1
Hyponephele lycaon	<0.01	0.02	0.886	225	-0.9318
Kanetisa circe	0.6	25.74	<0.001	166	38.56
Lycaena alciphron	0.3	7.6	0.013	167	22.23
Lycaena virgaureae	0.07	1.22	0.285	202	10.06
Melanargia lachesis	0.49	29.37	<0.001	174	22.74
Melitaea cinxia	0.25	1.36	0.308	129	23.96
Pyronia bathseba	0.46	6.88	0.030	138	47.05
Pyronia tithonus	0.53	16.93	0.001	192	22.01
Satyrus actaea	0.01	0.13	0.730	240	-3.1
Antocharis cardamines	0.71	38.52	<0.001	62	65.89
Brentis daphne	0.02	0.09	0.775	194	14.04
Glaucopsiche alexis	0.15	0.87	0.394	126	22.07
Zerynthia rumina	0.28	3.48	0.095	105	27.78
Tymelicus sylvestris	0.48	14.92	0.001	160	23.39
Tymelicus acteon	0.86	18.5	0.023	146	48.17
Pyronia cecilia	0.46	9.53	0.010	181	36.43

Table S3 Correlation table of the variables included in the analyses. We used non-parametric Spearman´s correlation coefficients to control for redundant variables. * $P < 0.05$; ** $P < 0.01$.

a) 2004 (*n* = 20 species)

		prevalence	Max altitude	Min altitude	Mean altitude	Altitudinal range	Global mean date	Unstandardized Residual
Prevalence	Correlation coefficient	1.000						
	Sig. (bilateral)	.						
Max altitude	Correlation coefficient	0.389	1.000					
	Sig. (bilateral)	0.090	.					
Min altitude	Correlation coefficient	-0.415	0.524(*)	1.000				
	Sig. (bilateral)	0.069	0.018	.				
Mean altitude	Correlation coefficient	0.053	0.880(**)	0.831(**)	1.000			
	Sig. (bilateral)	0.824	<0.001	<0.001	.			
Altitudinal range	Correlation coefficient	0.829(**)	0.599(**)	-0.202	0.272	1.000		
	Sig. (bilateral)	<0.001	0.005	0.392	0.246	.		
Global mean date	Correlation coefficient	0.354	0.365	0.272	0.373	0.119	1.000	
	Sig. (bilateral)	0.126	0.113	0.246	0.105	0.617	.	
Unstandardized Residual (globa mean date vs mean altitude)	Correlation coefficient	0.367	0.047	-0.017	0.024	0.102	0.892(**)	1.000
	Sig. (bilateral)	0.111	0.845	0.942	0.920	0.670	<0.001	.

b) 2005 (*n* = 24 species)

		prevalence	Max altitude	Min altitude	Mean altitude	Altitudinal range	Global mean date	Unstandardized Residual
Prevalence	Correlation coefficient	1.000						
	Sig. (bilateral)	.						
Max altitude	Correlation coefficient	0.469(*)	1.000					
	Sig. (bilateral)	0.021	.					
Min altitude	Correlation coefficient	-0.209	0.577(**)	1.000				
	Sig. (bilateral)	0.326	0.003	.				
Mean altitude	Correlation coefficient	0.273	0.900(**)	0.797(**)	1.000			
	Sig. (bilateral)	0.196	<0.001	<0.001	.			
Altitudinal range	Correlation coefficient	0.682(**)	0.548(**)	-0.172	0.294	1.000		
	Sig. (bilateral)	<0.001	0.006	0.423	0.163	.		
Global mean date	Correlation coefficient	0.435(*)	0.441(*)	0.279	0.543(**)	0.025	1.000	
	Sig. (bilateral)	0.034	0.031	0.186	0.006	0.907	.	
Unstandardized Residual (global mean date vs mean altitude)	Correlation coefficient	0.473(*)	0.156	-0.090	0.191	0.018	0.877(**)	1.000
	Sig. (bilateral)	0.020	0.465	0.677	0.370	0.934	<0.001	.

c) 2006 (*n* = 29 species)

		prevalence	Max altitude	Min altitude	Mean altitude	Altitudinal range	Global mean date	Unstandardized Residual
Prevalence	Correlation coefficient	1.000						
	Sig. (bilateral)	.						
Max altitude	Correlation coefficient	0.676(**)	1.000					
	Sig. (bilateral)	<0.001	.					
Min altitude	Correlation coefficient	-0.004	0.517(**)	1.000				
	Sig. (bilateral)	0.982	0.004	.				
Mean altitude	Correlation coefficient	0.368	0.804(**)	0.873(**)	1.000			
	Sig. (bilateral)	0.050	<0.001	<0.001	.			
Altitudinal range	Correlation coefficient	0.772(**)	0.577(**)	-0.279	0.106	1.000		
	Sig. (bilateral)	<0.001	0.001	0.142	0.584	.		
Global mean date	Correlation coefficient	0.372(*)	0.322	0.091	0.272	0.211	1.000	
	Sig. (bilateral)	0.047	0.089	0.640	0.154	0.271	.	
Unstandardized Residual (global mean date vs mean altitude)	Correlation coefficient	0.285	0.152	-0.112	0.056	0.199	0.961(**)	1.000
	Sig. (bilateral)	0.134	0.430	0.562	0.771	0.302	<0.001	.

d) 2007 (*n* = 29 species)

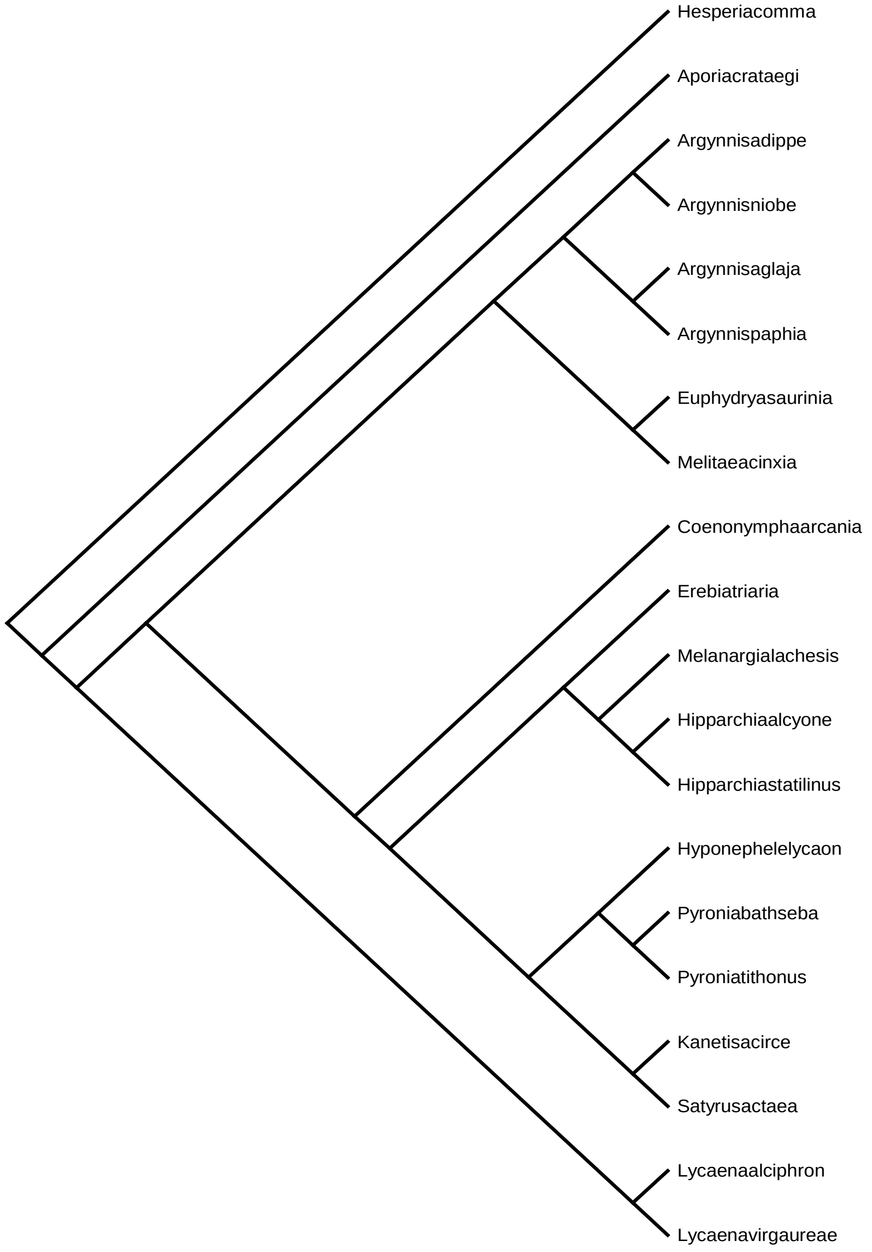
		prevalence	Max altitude	Min altitude	Mean altitude	Altitudinal range	Global mean date	Unstandardized Residual
Prevalence	Correlation coefficient	1.000						
	Sig. (bilateral)	.						
Max altitude	Correlation coefficient	0.481(**)	1.000					
	Sig. (bilateral)	0.008	.					
Min altitude	Correlation coefficient	-0.254	0.519(**)	1.000				
	Sig. (bilateral)	0.184	0.004	.				
Mean altitude	Correlation coefficient	-0.006	0.755(**)	0.913(**)	1.000			
	Sig. (bilateral)	0.977	<0.001	<0.001	.			
Altitudinal range	Correlation coefficient	0.848(**)	0.348	-0.529(**)	-0.252	1.000		
	Sig. (bilateral)	<0.001	0.064	0.003	0.188	.		
Global mean date	Correlation coefficient	0.302	0.587(**)	0.352	0.417(*)	0.226	1.000	
	Sig. (bilateral)	0.111	0.001	0.061	0.024	0.238	.	
Unstandardized Residual (global mean date vs mean altitude)	Correlation coefficient	0.390(*)	0.321	-0.104	-0.033	0.440(*)	0.849(**)	1.000
	Sig. (bilateral)	0.037	0.090	0.591	0.865	0.017	<0.001	.

e) 2008 (*n* = 27 species)

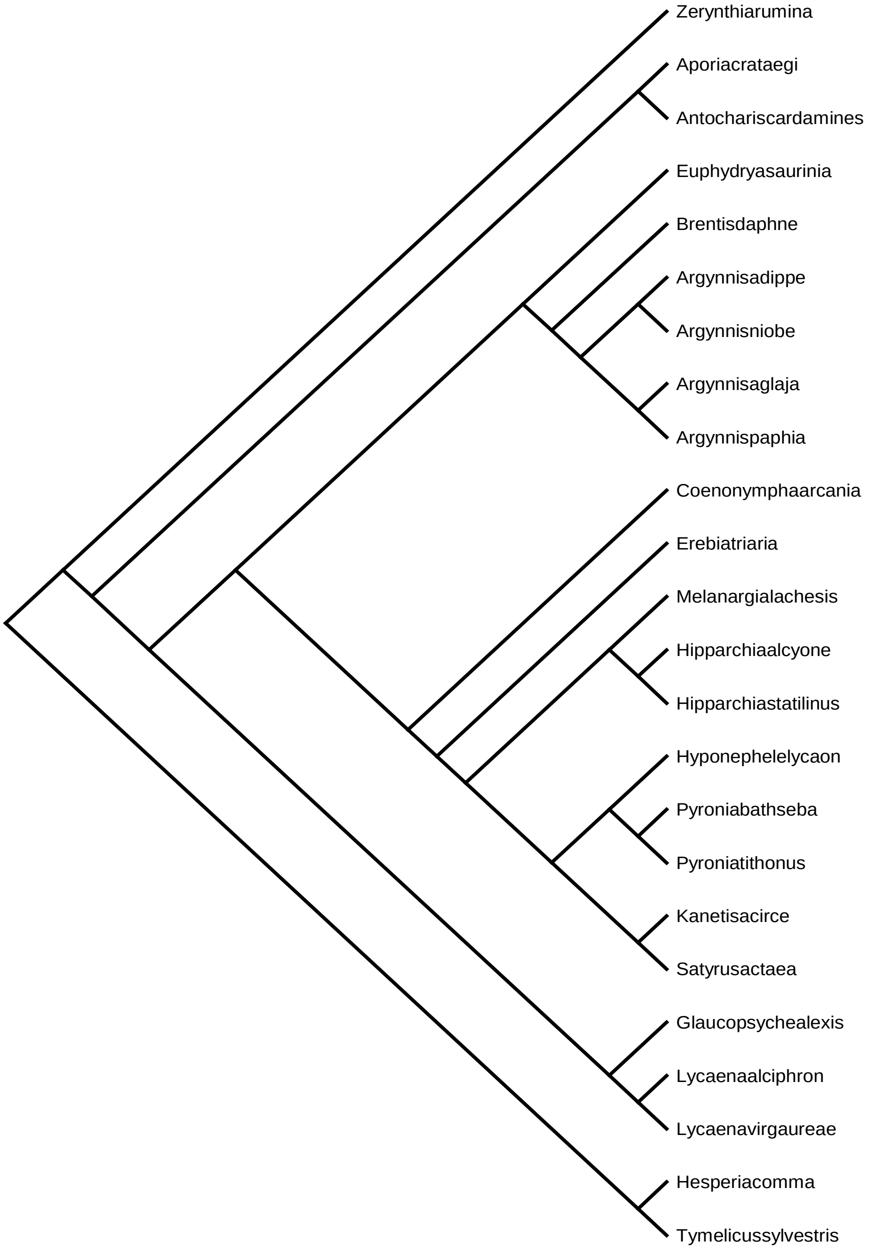
		prevalence	Max altitude	Min altitude	Mean altitude	Altitudinal range	Global mean date	Unstandardized Residual
Prevalence	Correlation coefficient	1.000						
	Sig. (bilateral)	.						
Max altitude	Correlation coefficient	0.462(*)	1.000					
	Sig. (bilateral)	0.015	.					
Min altitude	Correlation coefficient	-0.176	0.601(**)	1.000				
	Sig. (bilateral)	0.380	0.001	.				
Mean altitude	Correlation coefficient	0.159	0.868(**)	0.854(**)	1.000			
	Sig. (bilateral)	0.429	<0.001	<0.001	.			
Altitudinal range	Correlation coefficient	0.755(**)	0.569(**)	-0.268	0.160	1.000		
	Sig. (bilateral)	<0.001	0.002	0.177	0.426	.		
Global mean date	Correlation coefficient	0.385(*)	0.553(**)	0.291	0.415(*)	0.308	1.000	
	Sig. (bilateral)	0.048	0.003	0.142	0.031	0.118	.	
Unstandardized Residual (global mean date vs mean altitude)	Correlation coefficient	0.294	0.153	-0.058	-0.023	0.181	0.874(**)	1.000
	Sig. (bilateral)	0.137	0.446	0.773	0.911	0.366	<0.001	.

Figure S1 Phenology trees used in Phylogenetic regressions (PGLS) performed with COMPARE software.

a) 2004



b) 2005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Argynnisaglaja
Argynnispaphia
Coenonymphaarcania
Erebiatriaria
Melanargialachesis
Hipparchiaalcyone
Hipparchiastatilinus
Hyponephelelycaon
Pyroniabathseba
Pyroniatithonus
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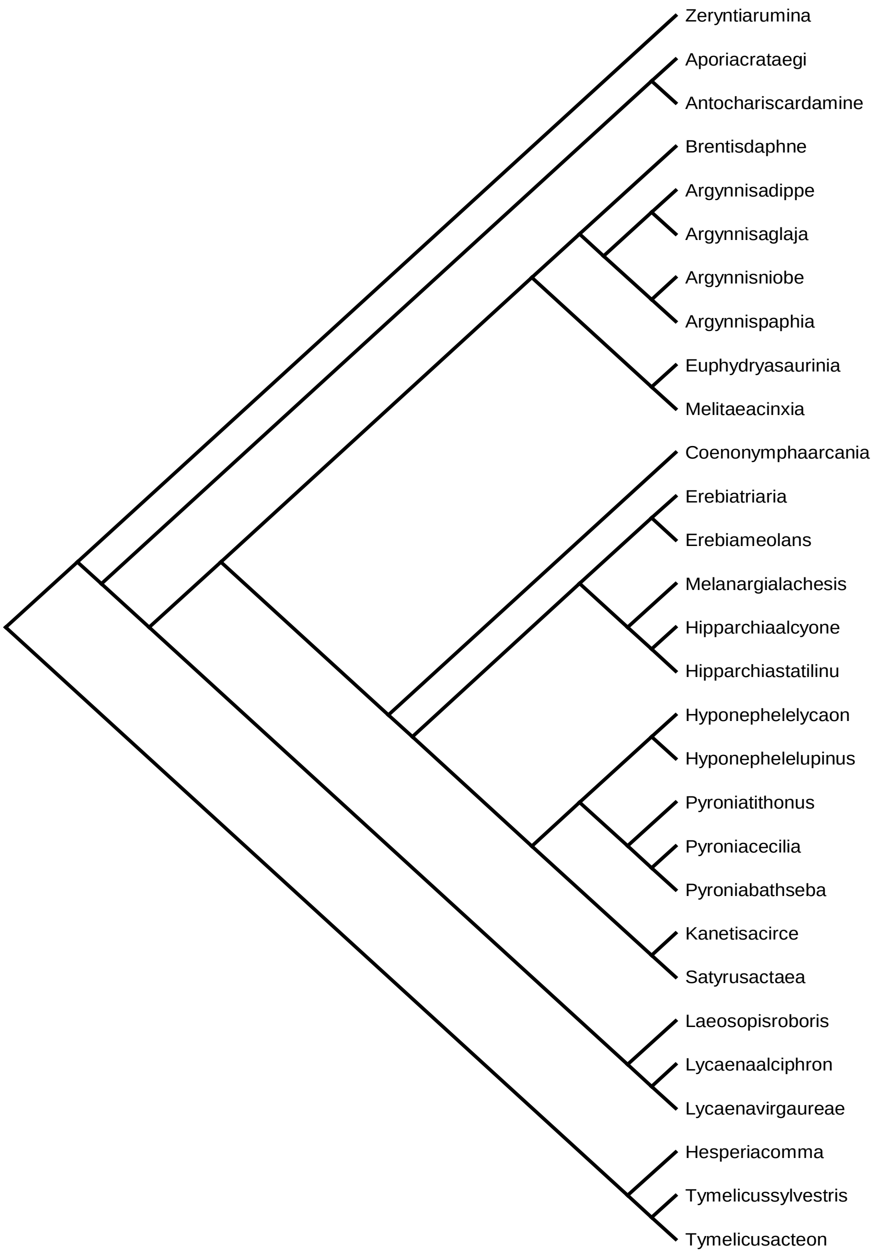
Glaucopsychealexis
Lycaenaalciphron
Lycaenavirgaureae
Hesperiacomma
Tymelicussylvestris

c) 2006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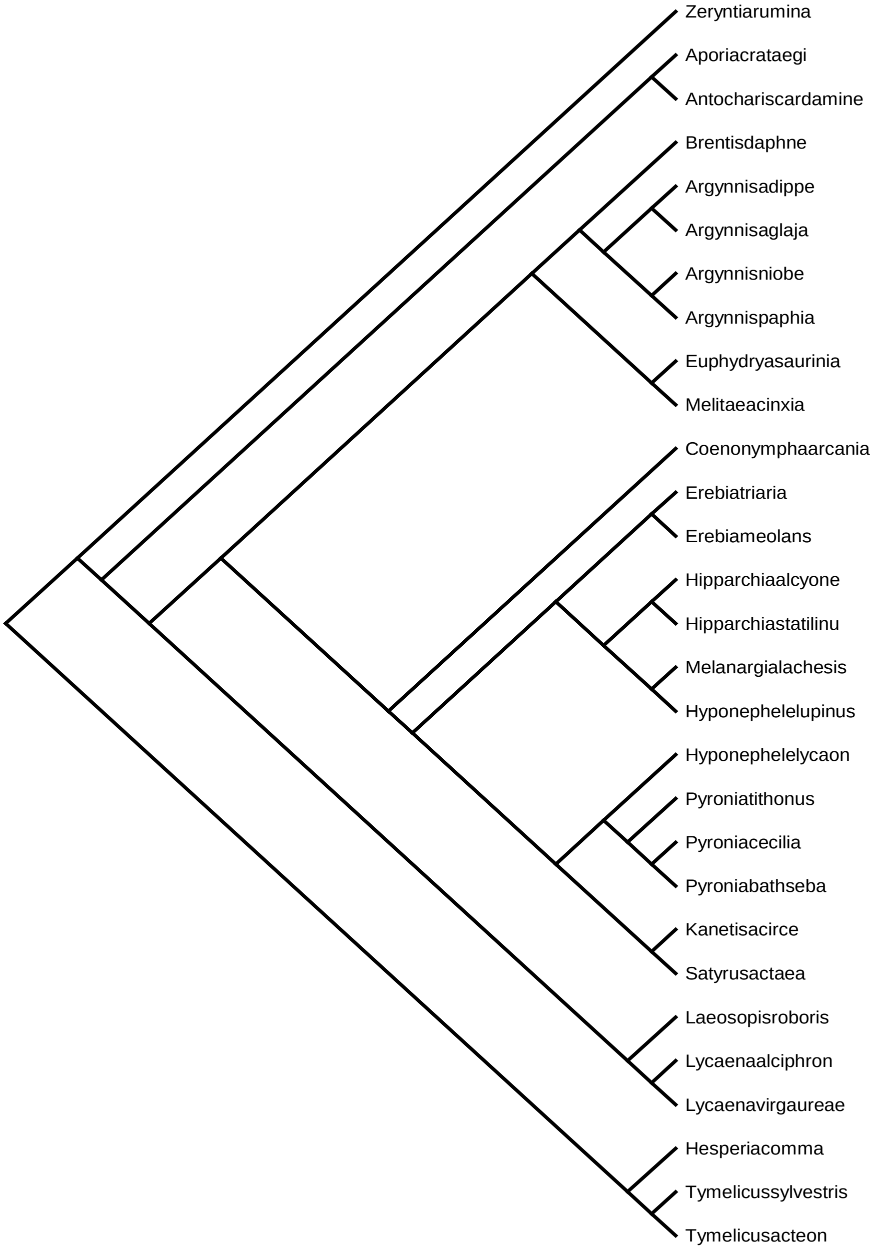
d) 2007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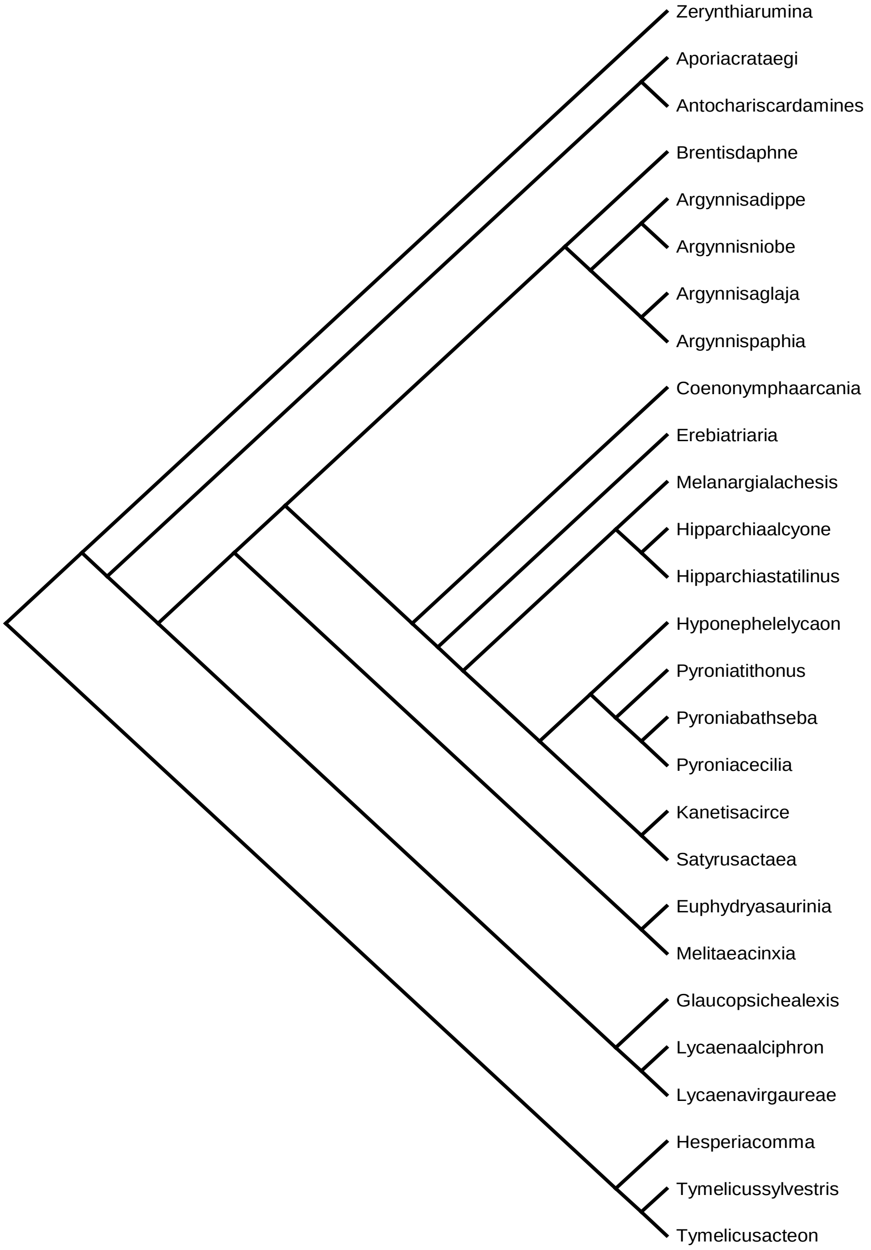
e) 2008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Conclusiones generales

-La distribución de varias especies de mariposas de la Sierra de Guadarrama se ha visto desplazada hacia altitudes superiores en el curso de los últimos 35 años. Este desplazamiento se ha reflejado en aquellas especies restringidas a zonas de montaña, en las que se detectó un ascenso de 212 m en su límite altitudinal inferior acorde con el incremento de 1.3°C en la temperatura regional sufrido durante el mismo periodo. Por lo tanto, las especies de montaña están ya manifestando las consecuencias del cambio climático reciente, cuya principal amenaza es la pérdida de área climáticamente habitable.

-Los factores topoclimáticos resultaron más importantes que los de cobertura del terreno a la hora de predecir la distribución y abundancia de las especies en una zona de alta variabilidad topográfica como la Sierra de Guadarrama. Por ello, los modelos basados únicamente en variables topoclimáticas podrían ser una herramienta adecuada para predecir los cambios potenciales en la distribución de especies en escalas regionales bajo las diversas situaciones de cambio climático propuestas por los modelos de circulación general.

-Los factores topoclimáticos tuvieron también una mayor contribución relativa que los de cobertura del terreno a la hora de predecir la riqueza de especies, mientras que en el caso de la composición de especies ambos tipos de factores tuvieron una importancia similar. Por lo tanto, es muy probable que el calentamiento climático futuro tenga un papel relativo más importante que los cambios en los usos de suelo sobre las posibles alteraciones de la riqueza específica de las comunidades de mariposas y esto podría traducirse en futuras pérdidas de diversidad durante las próximas décadas.

-Las fechas de vuelo de las mariposas sufrieron un retraso medio de unos 20 días por cada mil metros de ascenso en altitud. Sin embargo, se encontraron diferencias interespecíficas importantes en la magnitud de dicho retraso, de manera que es prácticamente inexistente en el caso de aquellas especies que vuelan a finales del verano y que tienen una distribución restringida a las partes más altas de la Sierra. La ausencia de retraso apunta a la posibilidad de que haya adaptaciones de las poblaciones de esas especies a las condiciones microclimáticas locales.

-Sería esperable que las especies que presentan adaptaciones locales en su fenología fueran capaces de experimentar reajustes de la misma ante los cambios futuros del clima. Sin embargo, dichas adaptaciones podrían suponer una desventaja si responden a estímulos físicos no directamente relacionados con el clima como el fotoperiodo, sobre todo ante la situación de cambio climático rápido proyectado por los modelos de circulación general.

General conclusions

-The distributions of several species of butterflies of the Sierra de Guadarrama mountain range have shifted upwards to higher elevations during the last 35 years. These changes have been most pronounced in species restricted to higher elevations, where we detected an elevational shift of 212 metres in their lower elevational limit, accompanying a rise of 1.3ºC in regional temperature recorded during the same period. Therefore, mountain species are already showing the consequences of ongoing climate change, with the main threat to their persistence being the loss of climatically suitable habitats

-Topoclimatic factors, rather than land cover, were the main determinants of species distributions and abundance in the topographically diverse Sierra de Guadarrama, where climate conditions vary markedly over relatively short distances. Thus, pure topoclimatic models could be an appropriate tool for predicting potential range shifts of species distributions at regional or local scales, based on climate change scenarios currently proposed by General Circulation Models (GCMs).

-In agreement with the results for species distributions and abundance, topoclimatic factors were also comparatively more important than land cover in determining species richness. However, topoclimate and land use factors each explained similar proportions of variation in patterns of species composition. Therefore it is plausible that present climate warming will play a role in influencing changes to the species richness of butterfly communities, which may cause biodiversity loss in the coming decades

-Flight dates of many species of butterflies were related to elevation, with an ascent of 1 kilometre implying a delay of approximately 20 days in average flight date. However, we found species-specific discrepancies in the magnitude of these delays. The relationship was strongest in species with earlier flight periods, and in species that did not fly at high elevations. In contrast, the flight dates of late-summer or high-elevation species did not change with elevation, suggesting local adaptations of these populations to local climates.

-Species which are able to synchronise their phenology across elevations might be able to adapt to changing climates in the future. However, the mentioned adaptations could also prove maladaptive under future climate conditions, if they are based on proxies of climate or microclimate, like photoperiod. These effects could even be exacerbated if the rapid climate warming projected by GCMs becomes true.

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