

Effects of wildfire on endemic breeding birds in a *Pinus canariensis* forest of Tenerife, Canary Islands¹

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Abstract: Fire is a key ecological force in pine forests worldwide, and faunal responses to this disturbance have been a major topic of ecology, yet little is known for oceanic island environments. Using line transects we surveyed the bird community of a natural *Pinus canariensis* forest burned in the summer of 2007 on Tenerife, Canary Islands, Spain. Our goal was to identify important environmental variables and the thresholds that influenced the pattern of bird abundance at the community, foraging guild, and species-specific level. Models were constructed by means of regression trees and cross validation applying the 1-SE rule. Mixed results were observed and only 2 species were clearly affected by fire severity. Overall, total bird abundance, total species richness, and total bird diversity were positively influenced by low, very low, and moderate canopy fire severity, respectively, and the presence of either *Erica* or *Myrica* shrubs. Consequently, high canopy fire severity had an overall negative effect on bird community characteristics. Abundance of *Myrica* shrubs affected positively general ground foragers such as common blackbird (*Turdus merula cabreræ*) and Canary Islands chiffchaff (*Phylloscopus canariensis*), a canopy forager. The number of thin trees was important for canopy foragers such as goldcrest (*Regulus regulus teneriffæ*) and African blue tit (*Cyanistes teneriffæ teneriffæ*), but also for a bark forager, the great spotted woodpecker (*Dendrocopos major canariensis*). European robin (*Erithacus rubecula superbus*) and the ubiquitous endemic blue chaffinch (*Fringilla teydea teydea*) were influenced by low and moderate canopy fire severity, respectively. We recommend that land managers incorporate these results into future post-fire management plans. Priority post-fire actions should be directed toward the protection and conservation of the endemic blue chaffinch, a species of conservation concern on the nearby island of Gran Canaria.

Keywords: breeding birds, Canary Islands, community ecology, fire, forest management, *Fringilla teydea*, Mediterranean, *Pinus canariensis*.

Résumé : Le feu est un agent écologique clé dans les pinèdes du monde entier et les réponses de la faune à cette perturbation sont un sujet d'étude majeur en écologie, cependant nous en savons peu concernant les environnements des îles océaniques. En utilisant des relevés par transect, nous avons étudié la communauté aviaire de forêts naturelles de *Pinus canariensis* brûlées à l'été 2007 sur Ténérife, dans les Îles Canaries, en Espagne. Notre but était d'identifier les variables environnementales importantes et les seuils qui influencent le patron d'abondance des oiseaux à l'échelle de la communauté, de la guildes des fourrageurs et au niveau de l'espèce. Nous avons construit des modèles à l'aide d'arbres de régression et de validation croisée en appliquant la règle de l'écart-type. Nous avons obtenu des résultats mitigés et seulement 2 espèces étaient influencées de façon évidente par la sévérité du feu. En général, l'abondance totale d'oiseaux, la richesse totale en espèces et la diversité aviaire totale étaient influencées de façon positive par les feux de canopée de sévérité faible, très faible et modérée, respectivement, et par la présence d'arbustes *Erica* ou *Myrica*. Par conséquent, les feux de canopée de sévérité élevée avaient dans l'ensemble un effet négatif sur les caractéristiques de la communauté aviaire. L'abondance d'arbustes *Myrica* influençait de façon positive les oiseaux se nourrissant généralement au sol comme le merle noir (*Turdus merula cabreræ*) et le pouillot des Canaries (*Phylloscopus canariensis*) qui se nourrit dans la canopée. Le nombre d'arbres de petit diamètre était important pour les oiseaux se nourrissant dans la canopée comme le roitelet de Ténérife (*Regulus regulus teneriffæ*) et la mésange des Canaries (*Cyanistes teneriffæ teneriffæ*), mais aussi pour une espèce se nourrissant dans l'écorce, le pic épeiche (*Dendrocopos major canariensis*). Le rouge-gorge de Ténérife (*Erithacus rubecula superbus*) et l'omniprésent pinson bleu endémique (*Fringilla teydea teydea*) étaient influencés par les feux de canopée de sévérité faible et modérée, respectivement. Il serait souhaitable que les gestionnaires du territoire intègrent ces résultats dans les futurs plans d'aménagement post incendie. Nous recommandons que les actions prioritaires post incendie soient orientées vers la protection et la conservation du pinson bleu endémique, une espèce dont le statut est préoccupant dans l'île voisine de Gran Canaria.

Mots-clés : aménagement forestier, écologie des communautés, feu, *Fringilla teydea*, Îles Canaries, Méditerranée, oiseaux nicheurs, *Pinus canariensis*.

Nomenclature: Ceballos & Ortuño, 1951; Snow & Perrins, 1998.

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Introduction

Today fire is recognized as an important ecological force or disturbance (Pyne, Andrews & Laven, 1997; DeBano, Neary & Ffolliott, 1998) that influences not only the structure and composition of floral and faunal communities (Whelan, 2001), but also population structures, resources, substrate availability, and the physical environment (White & Pickett, 1985). The remarkable variety of vertebrate responses to fire is well illustrated in the literature (Whelan, 2001; Hutto, 2006; 2008). Kikkawa, Ingram, and Dwyer (1979) suggested that the effects of fire on populations of vertebrates will depend on the various aspects of the fire regime: frequency, severity, extent, and season. In continental areas, some bird populations increase and others decrease as a result of fires (Whelan, 2001); hence birds respond both positively and negatively (Artman, Sutherland & Downhower, 2001; Kirkpatrick, Conway & Jones, 2006). Some species could even be considered to be burn specialists (*e.g.*, Lewis's woodpecker, *Melanerpes lewis*; Saab & Vierling, 2001). Meanwhile, the losses that fire causes by killing avian wildlife directly (burning or suffocation) are considered to be negligible (Agee, 1993). Although much attention has been paid to vertebrate responses to fire both in North America (see Pope, Block & Beier, 2009 and references therein) and in the Mediterranean basin (Brotons, Herrando & Martin, 2004; Ukmar *et al.*, 2007; Battisti *et al.*, 2008), nothing is known for the volcanic archipelago of the Canary Islands.

Wildland fires and *Pinus* trees are closely linked over time and space because some species of this genus show specialized adaptations to fire across their natural ranges in the northern hemisphere (Richardson, 1998), including the Mediterranean basin (Barbero *et al.*, 1998). The endemic *Pinus canariensis* forests of the Canaries occupy 4 major islands (Tenerife, Gran Canaria, La Palma, El Hierro) (Ceballos & Ortuño, 1951), with a total area of 80000 ha (60% of the archipelago total area), and are home to endemic native birds, some of conservation concern, such as the blue chaffinch, *Fringilla teydea* (Garcia-del-Rey *et al.*, 2009). The Canary Islands pine is considered to be a key element for ecosystem stability and conservation (Martín-Esquível *et al.*, 1995). It is one of the few pines in the world able to resprout immediately after a fire (Climent *et al.*, 2004a,b) and can reach up to 800 y old (Génova & Santana, 2006).

Fire severity is the magnitude of fire impacts on natural ecosystems; it has been widely used to describe the effects of fire on the biota, soil, water system, etc. (Simard, 1991). In the Canaries, fire severity has recently been found to influence first-year pine seedling establishment (Otto *et al.*, 2010), understory plant composition (Arévalo *et al.*, 2001), and post-fire nutrient availability (Duran *et al.*, 2008; 2009; Rodríguez *et al.*, 2009). In the Mediterranean ecosystems high-severity fire regimes are common (Agee, 1998). Based on short-term data (1986–2006), these islands (Tenerife, Gran Canaria, La Palma, El Hierro) seem to have a “moderate-severity” fire regime (*i.e.*, fire-return interval between 10 and 70 y, medium patch size or area burned) according to Agee's classification (1998), and natural ignitions (lightning or volcanic activity) are today rare (0.46% for lightning),

most fires being human induced (del Arco *et al.*, 1992; de Nascimento *et al.*, 2009; Área de Incendios Forestales del Ministerio de Medio Ambiente, Instituto Canario de Estadística, Gobierno de Canarias). Although natural ignitions such as lightning account for much of the fire activity in many pine ecosystems around the world (Taylor, 1974), human activities (Richardson & Bond, 1991) have increased the frequency of fire events in some areas (*e.g.*, western United States [Saab & Powell, 2005], 99% increase in Japanese forests [Nakagoshi, Nehira & Takahashi, 1987]), but not in others (*e.g.*, eastern and central North America [Saab & Powell, 2005]).

In July 2007, a total of 24 700 ha of pine forest (17 000 on Tenerife and 7700 on Gran Canaria) burned in the Canarian archipelago. Fire is today considered an “ecological disaster” by Canary Islands' authorities (*i.e.*, regional government and respective islands' governments [Cabildos]), which are obliged both to invest in minimizing the risk of forest fire in order to protect the civil population and settlements and to fund expensive post-fire restoration actions. Fire in the nearby Mediterranean forests has been observed to act at the community, guild, and species level, altering total abundance patterns, particularly of those forest bird species that tend to decrease strongly in burned forests (Brotons, Herrando & Martin, 2004; Ukmar *et al.*, 2007; Battisti *et al.*, 2008). Therefore, understanding bird responses to disturbance (*i.e.*, wildfire) in the Canary Islands is important both for conservation purposes and for designing effective post-fire management programs. This study aims to identify the different thresholds of fire severity that alter the total bird abundance, total species richness and total diversity patterns of the avifauna at the community, foraging guild (ground-shrub *versus* canopy), and species-specific level. Based on our findings, priority post-fire forest management actions are suggested.

Methods

STUDY AREA

The study area is located on the northern, windward slope of Tenerife, within the Corona Forestal Natural Park (28° 18' 40" N, 16° 43' 19" W), ranging from 575 to 2200 m asl and occupying a total area of 11 458 ha (Figure 1). This natural pine forest area burned in 1983 and again on the 27th of July 2007 (*i.e.*, 24 y later). Comparable unburned stands were not available since only pine plantations were left unburned on the north of this island.

The only tree present in the community is the endemic Canary Islands pine (*Pinus canariensis*), but the plant species composition of the understory varies with altitude. The Canary Islands pine is a generalist tree that can occur from near sea level up to about 2300 m (Jiménez *et al.*, 2005) and is well adapted to fire (Climent *et al.*, 2004b). Its needles exhibit morphological drought adaptations (Grill *et al.*, 2004), and its cones and seeds vary in size with altitude (Gil *et al.*, 2002). However, *P. canariensis* is one of the few pines that are able to resprout as adult trees, from root collar and stems, immediately after a fire (Climent *et al.*, 2004b). Below *ca* 1400 m asl the understory is dominated by *Myrica faya* and *Erica arborea*, 2 native shrubby species that dominate the so-called *Erica-Myrica*

woody heath, distributed immediately below the pine forest on the windward slopes. Above this altitude the dominant shrub is *Chamaecytisus proliiferus*, an endemic legume well adapted to drier pine forest environments. Other species, such as *Cistus symphytifolius*, an endemic purple-flowering Cistaceae, and the natives *Daphne gnidium* and *Asphodelus aestivus* can occur at both altitudinal levels. This important difference in understorey composition is mainly due to the influence of the northeast trade winds, which provide

a moister environment, often covering lower areas with mist. The grass layer is composed of only a few annual and ruderal plant species such as *Trifolium ligusticum*, *T. arvense*, *T. scabrum*, *Vulpia myuros*, *Tuberaria guttata*, and *Wahlenbergia lobelioides*, and only under special conditions, such as open canopies in mature sites, can pine seedlings be observed. More information on vegetation composition for this area can be obtained from del Arco Aguilar, Perez de Paz & Wildpret (1987) and del Arco et al. (1991).

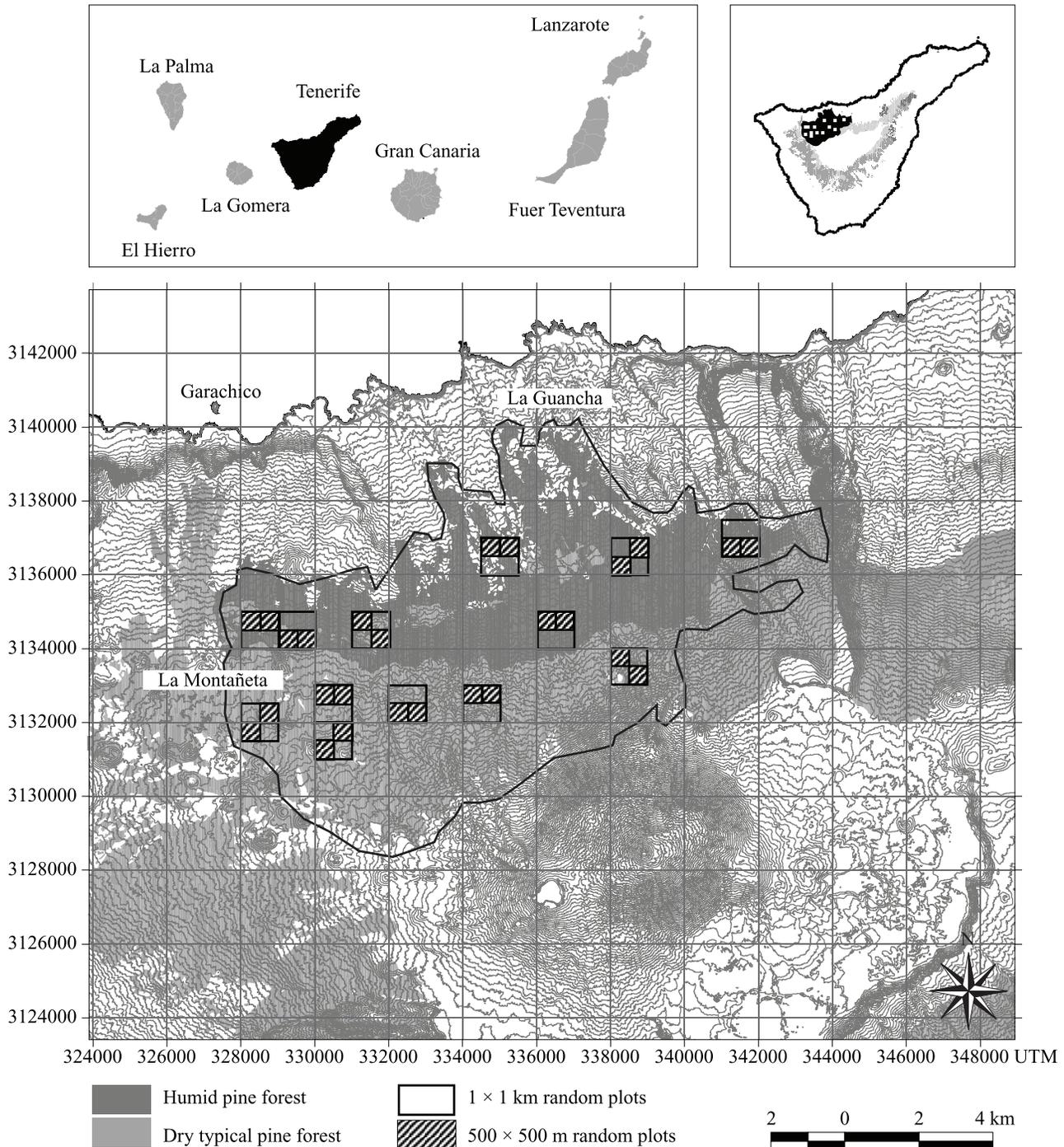


FIGURE 1. Study area showing the 2 types of forest burned in 2007 on the island of Tenerife and the plots and subplots sampled in the 2 y after the fire.

Several simplified systems have been developed to help categorize fire effects in different ecosystems. Based on fire severity, Agee (1993) used a broad classification for the effect of fire on the dominant vegetation (high, 100–80% burned; moderate; 79–50% burned; and low severity < 50% burned). Based on this classification and the degree to which vegetation is adapted to survive or regenerate after fire, the fire that started on the 27th of July 2007 and burned 17 000 ha in the northern region of Tenerife could be characterized as a high-severity surface fire (UFS, 75–100%, Table I) and a moderate-severity canopy fire (50–75%, Table I). The fire killed almost all individuals of the so-called “obligate seeder species”, and shrubs such as *Chamaecytisus proliferus* and *Cistus symphytifolius*, which withstand fires through the germination of their seed bank (Thanos & Georghiou, 1988), but it destroyed only the aerial parts of the so-called “resprouter species”, whose individuals possess the ability to resprout, either from the root crown through basal stems (*Erica* and *Myrica*) or from the trunk through epicornic stems (*Pinus*) after fire (Climent *et al.*, 2004b).

BIRD SURVEYS

A total of thirteen 1- × 1-km plots were selected randomly (7 in humid pine forest and 6 in dry pine forest) in the study area (Figure 1). On each plot, 2 subplots of 500 × 500 m were selected at random and a random 500-m

transect was aligned east to west. Each plot and its transect was considered a replicate in this study. The sampling protocol followed Bibby, Burgess, and Hill (2000) and Buckland *et al.* (2001). A single observer (EGDR) surveyed all transects walking at a uniform velocity (1.0–1.7 km·h⁻¹) depending upon terrain. All bird censuses were undertaken during May 2008 and again in May 2009, to coincide with the first and second breeding period of all the birds in the pine forest community of Tenerife after the fire (Garcia-del-Rey, 2003; Garcia-del-Rey & Cresswell, 2005; Garcia-del-Rey *et al.*, 2006). Birds observed and heard were identified to species level, and the perpendicular distance to the observer was estimated with the aid of a laser rangefinder (± 1 m error). No surveys were undertaken during rain or strong wind, and field work was only conducted between 0730 (dawn) and 1130 and between 1600 and 1930 (dusk) local time. The response variables were calculated as the number of each particular guild/bird species within each 500 m × (Effective Strip Width) m × 2; this allowed the index of abundance to be adjusted to abundance, after truncation and accounting for detection probability (for a detailed description of this procedure in DISTANCE Sampling methodology, see Buckland *et al.*, 2001). All bird taxonomy follows Snow and Perrins (1998), updated to accord with recent literature (*e.g.*, *Cyanistes teneriffae*; Dietzen *et al.*, 2008). Data from early morning and late afternoon censuses were pooled as there were no

TABLE I. Basic descriptive statistics of the variables measured per 500 m transect ($n = 52$). DBH = Diameter at breast height.

Variables	Description	Mean \pm SE	Min – Max
PREDICTOR VARIABLES			
Longitude	Longitude	-	-
Latitude	Latitude	-	-
Year	Nominal variable (1 = 2008, 2 = 2009)	-	-
Altitude	Mean altitude (m asl)	1401.25 \pm 21.29	1075 – 1700
Tree cover	Mean cover of pine tree (%)	19.15 \pm 2.21	1.40 – 58.00
T1	Number of trees with a DBH > 50 cm	0.74 \pm 0.12	0 – 4
T2	Number of trees with a DBH 50 – 25 cm	1.05 \pm 0.12	0 – 5
T3	Number of trees with a DBH < 25 cm	14.85 \pm 1.47	1 – 39
Myrica	Cover of “green” <i>Myrica faya</i> (%)	1.13 \pm 0.72	0 – 36
Erica	Cover of “green” <i>Erica arborea</i> (%)	2.84 \pm 1.26	0 – 56
Chama	Cover of “dead” <i>Chamaecytisus proliferus</i> (%)	10.29 \pm 2.57	0 – 63
Cist	Cover of “dead” <i>Cistus symphytifolius</i> (%)	2.08 \pm 0.81	0 – 28
Seed	Mean number of viable seeds on the ground	0.00 \pm 0.00	0 – 0
Seedling	Mean number of first year alive seedlings	0.94 \pm 0.26	0 – 10
CFS	Mean class of dead canopy cover (%) (1 = 0 – 25, 2 = 25 – 50, 3 = 50 – 75, 4 = 75 – 100)	2.76 \pm 0.13	1 – 4
UFS	Mean class of dead understorey cover (%) (1 = 0 – 25, 2 = 25 – 50, 3 = 50 – 75, 4 = 75 – 100)	3.93 \pm 0.03	3 – 4
RESPONSE VARIABLES (NUMBER OF OBSERVATION/CONTACTS)			
Total bird abundance (48/329)	Total number of birds present in 500-m transect	6.32 \pm 0.61	0 – 18
Total species richness (48/158)	Total number of species present in 500-m transect	3.04 \pm 0.23	0 – 7
Total bird diversity	Shannon – Weaver log 10 diversity index	1.60 \pm 0.33	0 – 2
Canopy foragers (41/149)	Total number of canopy foragers in 500-m transects	2.87 \pm 0.34	0 – 11
Ground-shrub foragers (26/60)	Total number of ground-shrub foragers in 500-m transects	1.15 \pm 0.22	0 – 7
Fritey (38/120)	Total number of <i>Fringilla teydea teydea</i>	2.31 \pm 0.32	0 – 9
Denmaj (14/20)	Total number of <i>Dendrocopos major canariensis</i>	0.38 \pm 0.09	0 – 2
Regreg (20/36)	Total number of <i>Regulus regulus teneriffae</i>	0.69 \pm 0.14	0 – 4
Phycan (13/22)	Total number of <i>Phylloscopus canariensis</i>	0.42 \pm 0.12	0 – 4
Eriub (14/22)	Total number of <i>Eriothacus rubecula superbus</i>	0.42 \pm 0.11	0 – 3
Turmer (14/22)	Total number of <i>Turdus merula cabrerae</i>	0.42 \pm 0.11	0 – 3
Cyaten (35/71)	Total number of <i>Cyanistes teneriffae teneriffae</i>	1.37 \pm 0.18	0 – 4
Sercan (10/16)	Total number of <i>Serinus canaria</i>	0.31 \pm 0.12	0 – 5
Fricoe (1/1)	Total number of <i>Fringilla coelebs canariensis</i>	0.01 \pm 0.09	0 – 1

statistical differences between these 2 time periods in the response and predictor variables ($P > 0.1$). Data from the 2 y of study were also pooled as no significant inter-annual variation in bird abundance was observed. Note that year has been included as a nominal variable in Table I.

For the purpose of this study the foraging guilds were defined as follows: ground-shrub foragers included common blackbird (*Turdus merula cabreræ*), European robin (*Erithacus rubecula superbis*), and Atlantic canary (*Serinus canaria*). Canopy foragers included Canary Islands chiffchaff (*Phylloscopus canariensis*), African blue tit (*Cyanistes teneriffae teneriffae*), and goldcrest (*Regulus regulus teneriffae*). Great spotted woodpecker (*Dendrocopos major canariensis*) was considered a bark forager, and the endemic blue chaffinch (*Fringilla teydea teydea*) was treated as a ubiquitous species because females forage in the canopy while males forage on the ground during the breeding season (Garcia-del-Rey & Cresswell, 2005).

HABITAT STRUCTURE

A total of 15 environmental variables (plus year, Table I) were measured by EGDR within a radius of 25 m centred every 100 m along each 500-m transect and averaged. A laser rangefinder (± 1 m error) was used to aid estimation of the radius from the observer. All predictor variables were selected considering the most important ecological requirements of the birds in this pine forest in terms of foraging habitat preferences (*i.e.*, ground, bark, canopy, shrub, etc.) (Snow & Perrins, 1998).

Survey points every 100 m along each 500-m transect were geo-referenced (longitude, latitude, and altitude) with a Garmin 12 GPS with a precision of 1 m by means of the average location function. Tree cover (%) was measured with a spherical convex densitometer (Lemmon, 1956;

1957) (4 readings coinciding with north, south, east, and west), whereas the number of pine trees of specific diameters at breast height (DBH) (T1, > 50 cm; T2, 50–25 cm; T3, < 25 cm) and the cover of *Myrica*, *Erica*, *Chamaecytisus*, and *Cistus* were estimated visually. The number of viable pine seeds on the ground (Seed) and the number of first-year alive seedlings (Seedling) were counted in 1- × 1-m plots located every 100 m along each 500-m transect (seeds were crushed to check for possible viability as suggested in Newton, 2007).

Canopy fire severity (CFS) and understorey fire severity (UFS) were estimated visually every 50 m along each 500-m transect within a radius of 25 m of the observer and averaged per transect. Estimates were made not by standing under the trees, but from the centre of the circumference sampled. Fire severity has been defined in terms of fire effects on vegetation cover (Pyne, Andrews & Laven, 1997). Hence, canopy fire severity was determined according to the degree of needle loss due to crown damage, based on a visual estimate of the percentage of green needles left at the top of the crown with respect to the whole crown (*i.e.*, 100% CFS = 100% loss of green needles); the same methodology was applied to the leaves of the understorey. Newly sprouted green needles were easily identified and observed from below during the years of the study (brush-like shape, Ceballos & Ortuño, 1951) and were not included in the estimates.

STATISTICAL ANALYSES

The potential intercorrelations (*i.e.*, collinearity) between variables were examined using Spearman’s rank correlation tests (Table II). When 2 variables had a cross-correlation ≥ 0.8 one was removed (*i.e.*, latitude *versus* altitude, see Table II; the former was removed from all the multivariate analyses) (Zuur, Ieno & Smith, 2007). Moran’s *I* index and

TABLE II. Summary results of every cross-validation of the different full regression trees used for modelling the habitat preferences of the avifaunal community per every 500-m transect ($n = 52$) (see Appendix I for figures of full results). CFS = Canopy Fire Severity, low (1 = 0–25%, 2 = 25–50%), moderate (3 = 50–75%), high (4 = 75–100%).

Most important predictor	Response variables	Regression tree model result	Cross-validation error	% variance explained	Foraging stratum
INFLUENCED BY CANOPY FIRE SEVERITY					
	Total bird abundance	CFS ≤ 2 (0–50%); <i>Myrica</i> > 1.5	1.10	65	-
	Total species richness	<i>Erica</i> > 2.5; CFS ≤ 1 (0–25%)	1.16	73	-
	Total bird diversity	CFS ≤ 3 (0–75%); <i>Erica</i> > 2.5	1.60	30	-
	<i>Fringilla teydea teydea</i>	CFS ≤ 2 (0–50%)	0.79	27	Ground-shrub/ Canopy
	<i>Erithacus rubecula superbis</i>	CFS ≤ 3 (0–75%); Tree cover > 32; T2 ≤ 0.5	1.20	44	Ground-shrub
NOT INFLUENCED BY CANOPY FIRE SEVERITY					
Influenced by “green”					
	<i>Myrica faya</i>	<i>Turdus merula cabreræ</i>	1.20	66	Ground-shrub
		<i>Phylloscopus canariensis</i>	1.20	19	Canopy
		Ground-shrub foragers	1.40	49	Ground-shrub
Influenced by “dead”					
	<i>Chamaecytisus proliiferus</i>	<i>Serinus canaria</i>	1.40	51	Ground-shrub
Influenced by number of trees with a DBH >25					
	<i>Dendrocopos major canariensis</i>	T3 = 5.5–8.5	1.50	38	Bark
	<i>Regulus regulus teneriffae</i>	T3 > 21.5	0.84	43	Canopy
	<i>Cyanistes teneriffae teneriffae</i>	T3 > 16	1.40	15	Canopy
	Canopy foragers (excluding <i>Fringilla teydea</i>)	T3 > 16	1.40	53	Canopy

a permutation test were used to test for autocorrelation in the spatial data.

Regression trees (Zuur, Ieno & Smith, 2007), a powerful technique in ecology, were used to model the influence of habitat features on bird abundance in order to explore the relationship between a single response variable and multiple explanatory variables (Chambers & Hastie, 1992; De'Ath & Fabricus, 2000). A regression tree is created by the process of repeatedly partitioning the observations to maximize the between-group dissimilarity while simultaneously reducing the within-group sample heterogeneity, based on the values (order) of an explanatory variable. This is critical for the scope of this study because regression trees can identify the different classes of fire severity to which the different bird species are responding, as well as their relative importance to other environmental variables. Tree models also deal better with non-linearity and interaction between explanatory variables than regression, generalized linear models (GLM), and generalized additive models (GAM) and can be used to find interactions missed by other methods in ecological studies (Zuur, Ieno & Smith, 2007). Another advantage is that regression trees are not affected by transformation of the explanatory variables (Zuur, Ieno & Smith, 2007) and minimize the problems of stepwise (forward and backward) procedures, which are becoming less popular among ecologists today (Whittingham *et al.*, 2006). The predictive power of the obtained regression tree was evaluated by means of a cross-validation procedure using 10 random sampling iterations and applying the 1-SE rule. This enables objective selection of optimal tree size and avoids complex suboptimal trees (for a full explanation of this procedure, see Zuur, Ieno & Smith, 2007).

Brodgar 2.5.6. (www.brodgar.com) and R (www.r-project.org) were used for all univariate analyses. Simple descriptive statistics follow Zar (1998).

Results

On average the most abundant species were the *Fringilla teydea teydea* (a ground-shrub/canopy forager) and *Cyanistes teneriffae teneriffae* (2.31 versus 1.37 bird·0.5 km⁻¹; Table I). Intermediate values were observed for 3 ground-shrub foragers (*Turdus merula cabrerae*, *Erithacus rubecula superbus*, *Serinus canaria*), 2 canopy foragers (*Phylloscopus canariensis*, *Regulus regulus teneriffae*), and a bark forager (*Dendrocopos major canariensis*). Very low values were obtained for *Fringilla coelebs canariensis*, a ground-shrub forager. Hence, canopy foragers were more abundant on average than ground-shrub foragers.

Collinearity (> 0.8) was found between altitude and latitude, and therefore the latter was removed from the analyses. Moran's *I* index for total bird abundance was 0.178, and the result of the permutation test was not significant ($P = 0.06$). None of the other response variables gave a significant result; hence, no spatial autocorrelation was observed between transects. Table II summarizes the results of the most optimal tree models obtained by cross-validation and by applying the 1-SE rule when data allowed for this (see Appendix I for figures of full results).

INFLUENCED BY FIRE SEVERITY

Overall, total bird abundance, total species richness, and total bird diversity were influenced by canopy fire severity, although at different intensities, and *Fringilla teydea* and *Erithacus rubecula* were the only bird species that responded to canopy fire severity (Table II; Appendix I).

The highest bird abundance was recorded in areas of pine forest with a low canopy fire severity (≤ 2 , 0–50%) and a “green” *Myrica* shrub layer greater than average (> 1.5%) (Table II). Conversely, no birds were found in areas where all of the following conditions occurred: moderate to high canopy fire severity (CFS > 50%), shrub layer cover of “dead” *Chamaecytisus* between 26 and 52.5%, “green” *Erica* cover lower than 1.5%, and no mature trees (T1 < 0.5) (Appendix I) (CV error = 1.1, 65% variance explained).

Maximum species richness was observed in the humid pine forest, with “green” *Erica* cover being the most important predictor (> 2.5%) and very low canopy fire severity the second most important (CFS < 25%) (Table II) (CV error = 1.16, 73% variance explained).

Results of the regression tree applied to the Shannon–Weaver diversity index suggest that diversity was highest in areas of low to moderate canopy fire severity (CFS < 75%) with a “green” *Erica* cover greater than 2.5% (Table II) (CV error = 1.6, 30% variance explained).

The endemic *Fringilla teydea* was positively influenced by low severity (low + moderate) (Table II; Appendix I) (CV error 0.79, 27% variance explained) and negatively influenced by high severity. Moderate canopy fire severity (CFS < 75%) had a negative effect on the abundance of *Erithacus rubecula* (Table II; Appendix I) (CV error 1.2, 44% variance explained).

NOT INFLUENCED BY FIRE SEVERITY

Two species were positively influenced by the cover of “green” *Myrica* shrubs (*Turdus merula*, *Phylloscopus canariensis*), 1 by the cover of “dead” *Chamaecytisus* shrubs (*Serinus canaria*), and the rest by the number of thin pine individuals (*Dendrocopos major*, *Regulus regulus*, *Cyanistes teneriffae*) (see Table II for CV error and % variance explained and Appendix I for figures of full results).

From a foraging guild perspective (excluding *Fringilla teydea*), the abundance of ground-shrub foragers responded positively to “green” *Myrica* cover (> 2.5%), whereas the number of thin pine trees was the most important predictor of the abundance of canopy foragers (T3 > 16).

Discussion

In this study, we found “possible” mixed responses to fire in a relatively poor island bird community. We also found that most bird species were not significantly influenced by fire severity. Although total bird abundance, total species richness, and total bird diversity were influenced by canopy fire severity (low to moderate severity), only a few bird species contributed clearly to this observed pattern (*i.e.*, the endemic blue chaffinch, *Fringilla teydea teydea*, and the endemic race of European robin, *Erithacus rubecula superbus*). The variable responses among species immediately after fire have been explained in fire ecology theory in terms of the life-history

characteristics of the animals and their preferred habitats, because the impacts of fire on wildlife populations are largely mediated indirectly through changes in food, cover, and structural diversity (Whelan, 2001). Obviously, animals living in protected, unburned sites within a habitat are more likely to survive than those in exposed, burned areas. Recher and Christensen (1981) have suggested that unburned refuges provide the nucleus for recovery of animal populations after fire, and the patchiness of fire has also been stressed in interpreting bird population dynamics in the past (Whelan, 2001). Our general results seem to support the high variation in responses found in other studies of forest bird communities both in North America (Hutto, 2006; Kirkpatrick, Conway & Jones, 2006; Koivula & Schmiegelow, 2007; Kotliar, Kennedy & Ferree, 2007; Haney, Apfelbaum & Burris, 2008) and in the Mediterranean basin (Brotos, Herrando & Martin, 2004; Ukmar *et al.*, 2007; Battisti *et al.*, 2008).

Studies on fire and avian ecology in North America reveal interesting patterns in the responses of birds to fire. Saab & Powell (2005) suggested that ground and bark insectivores are clearly favoured by recently burned habitats, whereas foliage gleaners are not. The present study supports this pattern, because not all ground-shrub foragers favoured burned areas (*e.g.*, European robin), and foliage gleaners (canopy foragers in this study) were not influenced by fire severity. The local importance of “green” *Myrica* shrub cover for ground foragers (such as common blackbird) and the chiffchaff, which tend to nest in shrubs (Snow & Perrins, 1998), is highlighted by this study.

In the Mediterranean basin, pine forest avian species tend to decline strongly in terms of richness and abundance in burned areas (Ukmar *et al.*, 2007; Battisti *et al.*, 2008). Our results for the European robin (*Erithacus rubecula superbus*) are striking as this is mainly a “monteverde” (*Myrica/Erica* woody heath and laurel forest) bird species that exploits the shrub and ground layers and occurs at lower densities in mixed pine forests (Snow & Perrins, 1998). In continental Mediterranean areas, this species prefers sites that include elements of cool shade, moisture, and medium tree height and density (Snow & Perrins, 1998). Our island results do not depart from these mainland preferences, as we found higher abundances of this insectivore in areas where the canopy fire severity was low or even moderate and pine tree cover was greater than 32% but not in areas with high *Myrica* cover, as expected. This observed pattern could be a result of fire causing a significant reduction in canopy density and hence conditions of cool shade and moisture.

Although we were not able to sample controls of unburned forests, our results for the endemic blue chaffinch (*Fringilla teydea teydea*) agreed with findings in studies in mainland areas and Mediterranean continental islands for other pine forest species. For example, the effects of fire, *i.e.*, reductions in canopy volume and the quantity of pine seeds, have been suggested as an explanation for a decrease in a forest island endemic bird, the Corsican nuthatch (*Sitta whiteheadi*), after a fire (Moneglia *et al.*, 2009). Another recent study (Russell *et al.*, 2009) reported that pine seed specialists such as Clark’s nutcracker (*Nucifraga columbiana*) and pine siskin (*Carduelis pinus*) declined

after prescribed fire treatments in western United States. Our findings agree with these results, as the blue chaffinch was negatively influenced by moderate to high canopy-fire severity (> 50%). This finch, a species of conservation concern on the nearby island of Gran Canaria, where the entire forest range was burned in 2007, only inhabits the *Pinus canariensis* forests of these 2 islands. Pine seeds are its main food resource when available during the summer and fall (Garcia-del-Rey *et al.*, 2009), but *Myrica* seeds are also exploited during the winter (Garcia-del-Rey & Cresswell, 2005). Insects such as caterpillars prey on the pine needles and on the fresh leaves of *Chamaecytisus* shrubs during the spring and are an important part of the chaffinch nestling diet (Garcia-del-Rey & Cresswell, 2005). The results of our study clearly demonstrate that both food availability and habitat structure for this endemic bird species have suffered a profound change, at least during the first 2 y post-fire. An important volume of canopy has been destroyed in some areas, and the dominant *Chamaecytisus* shrubs (an obligate seeder), which occur mainly in the higher dry forest, were all killed by the high-severity understory fire. Although pine trees tend to recover rapidly after a fire, several years will be needed for this legume to recover to pre-fire status.

The long-term relationship of fire and *Pinus canariensis* forest in the volcanic archipelago of the Canary Islands has been stressed in past studies (Ceballos & Ortuño, 1951; Climent *et al.*, 2004b), and a recent study suggests that natural pine regeneration does not occur in high-fire-severity areas (Otto *et al.*, 2010). Based on our findings, we hypothesize that the blue chaffinch is a pine seed eater specialist well adapted to low canopy-fire severity (0–50%). It is not yet clear if the great spotted woodpecker benefits from wildfire disturbance in the ways that have been found elsewhere (*e.g.*, Nappi & Drapeau, 2009). Future fire research should try to detect and study other fire regimes and severities in different size of burns, and also study pre-fire characteristics. Comparing similar burned and unburned pine forests is also necessary in this oceanic environment when conditions allow for such comparisons.

MANAGEMENT IMPLICATIONS

Pine forest management programs on this archipelago are currently being undertaken without considering bird responses to wildfire. Unlike typical post-fire management actions undertaken in both North America (Hutto, 1995; 2006) and the Mediterranean basin (Herrando *et al.*, 2009), no post-fire logging has been conducted in the Canary Islands, mainly because the number of trees that die due to fire has been negligible in the past. Hence, most post-fire actions are directed towards minimizing soil erosion, as in other Mediterranean areas (Ne’eman, 1997); such erosion can be severe during the first winter after disturbance, especially on highly inclined slopes and in areas covered with pyroclastics. Therefore, based on the results of the present study, we make the following recommendations:

- 1) It would be desirable to incorporate avifaunal responses to fire in future management plans. Areas of low canopy-fire severity that have *Myrica* shrubs should be protected if the objective is to benefit the overall bird abundance of the forest. However, we recommend that future management

plans should prioritize post-fire actions for the conservation of the endemic blue chaffinch (*Fringilla teydea*).

- 2) No post-fire management action that could impact on the low-severity areas (greener clumps of vegetation) should be undertaken within a buffer of 200 m from these optimal sites, particularly during the first and second breeding seasons (March–August) following a summer fire.

Acknowledgements

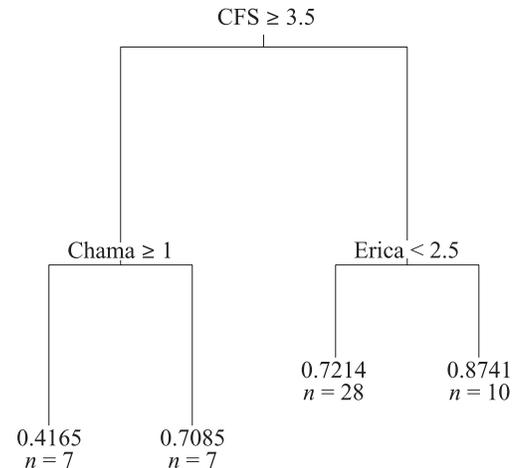
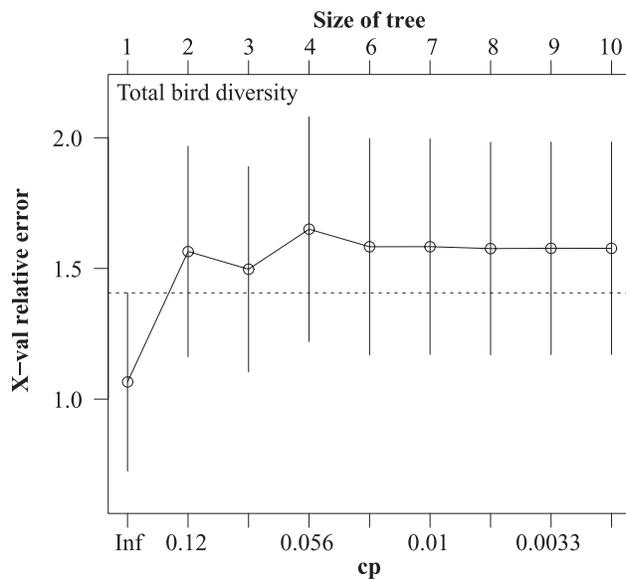
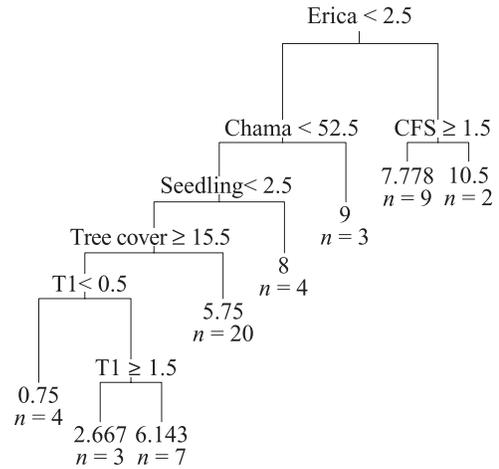
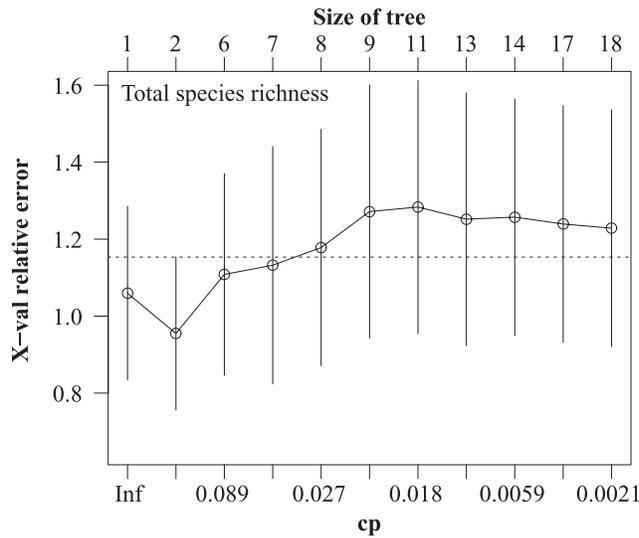
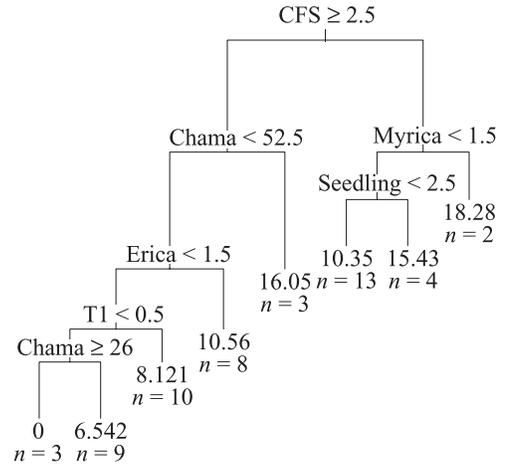
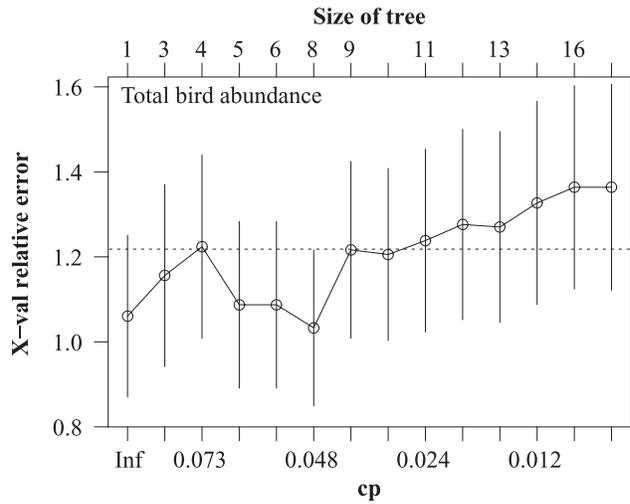
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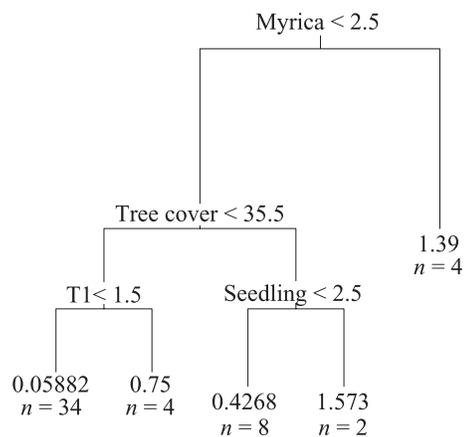
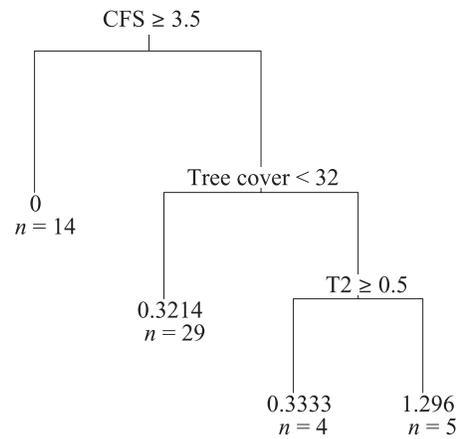
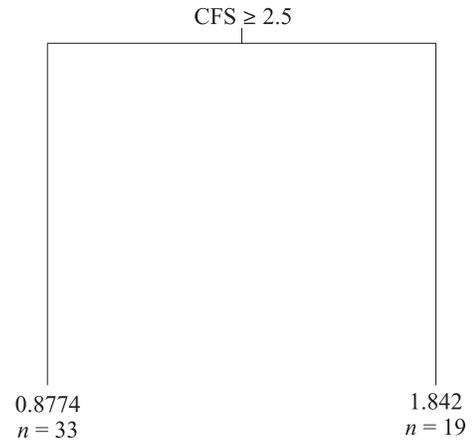
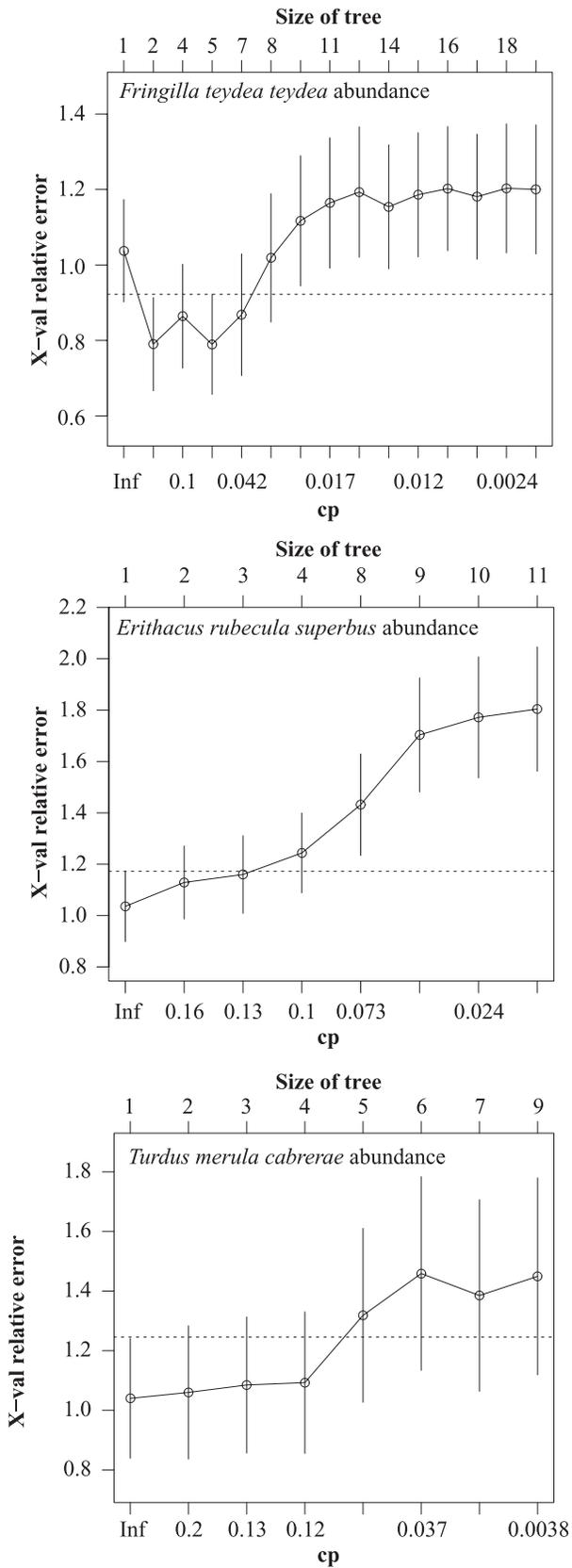
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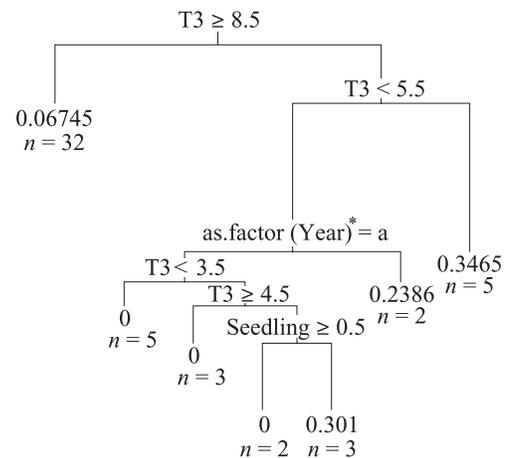
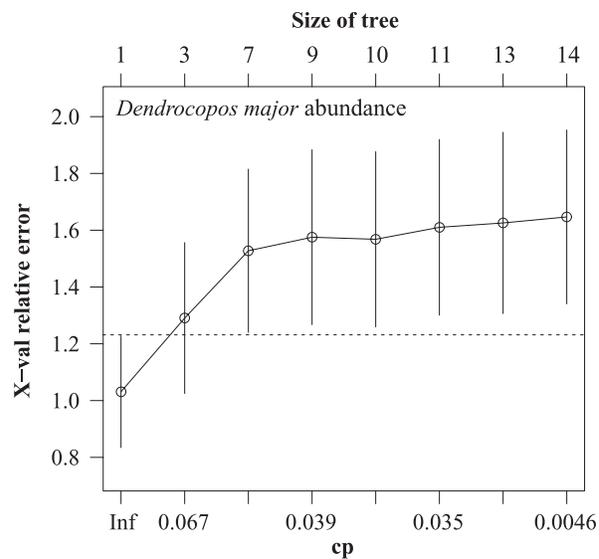
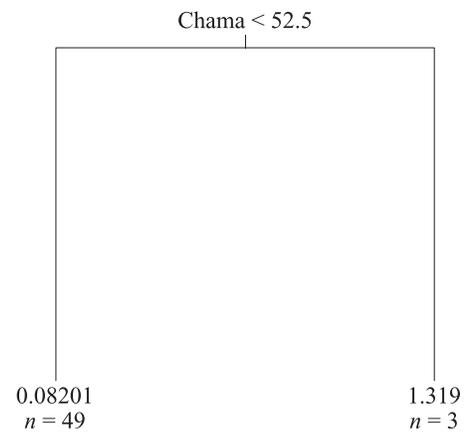
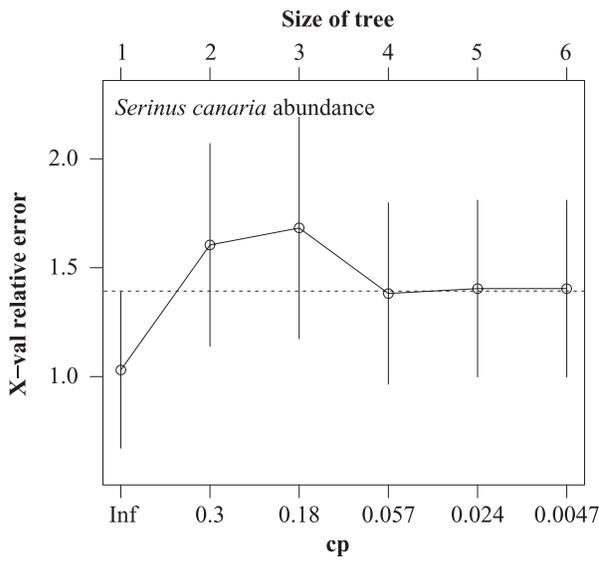
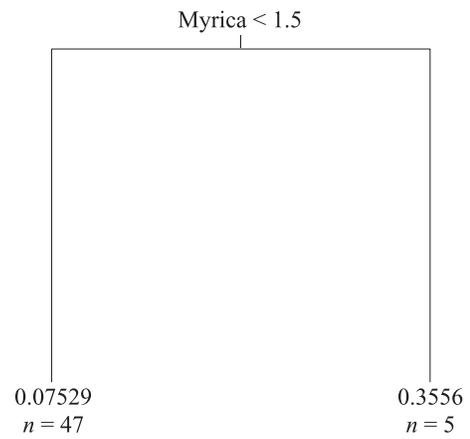
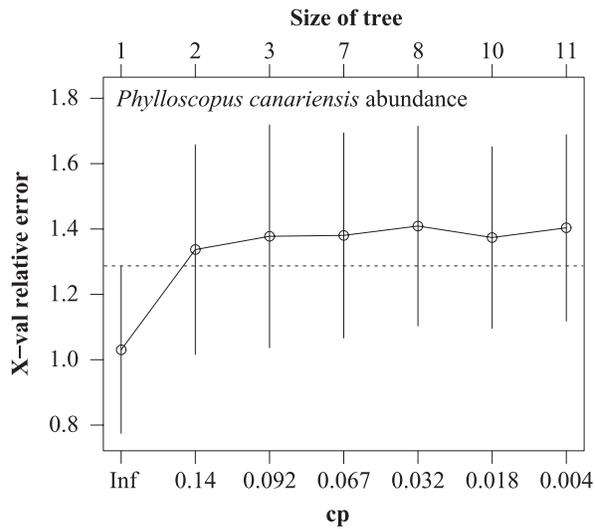
APPENDIX I. Cross-validation results (left) and pruned regression tree (right) models analyzing every response variable per every 500-m transect, $n = 52$. Branch length is proportional to the improvement of the fit. True statement = left, cp = complexity parameter.



APPENDIX I. continued.

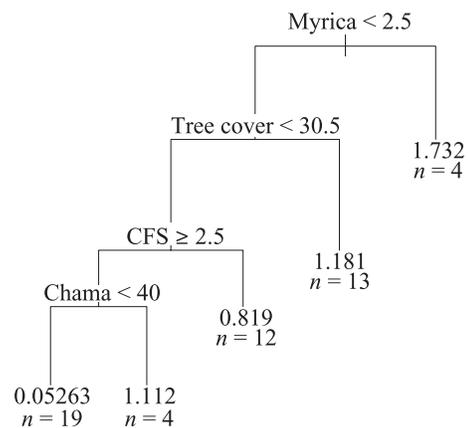
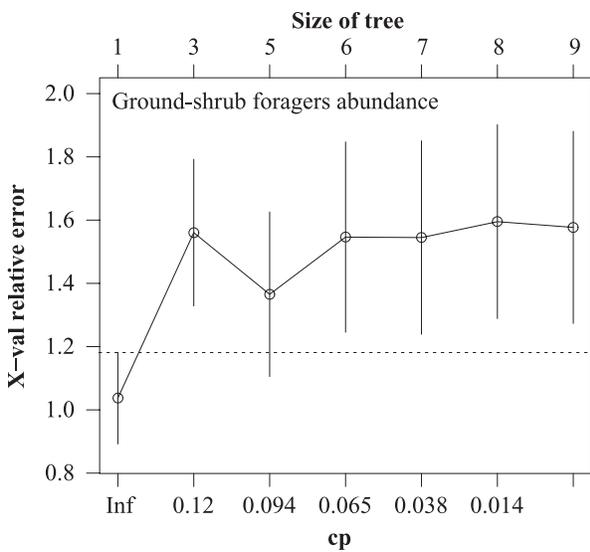
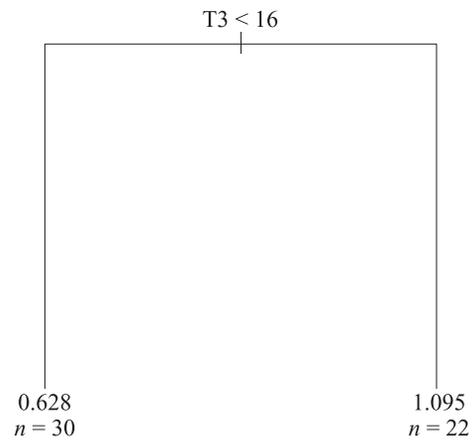
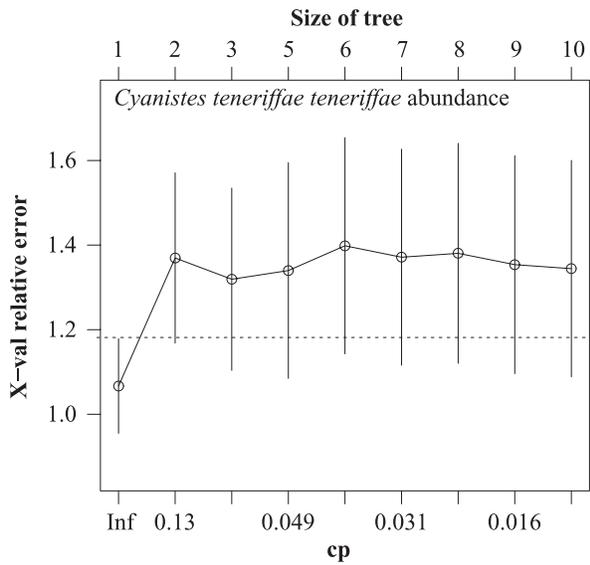
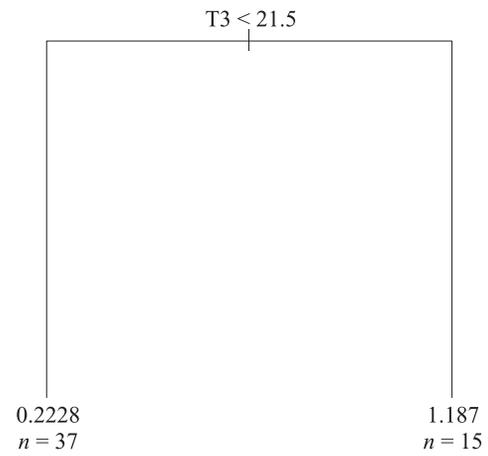
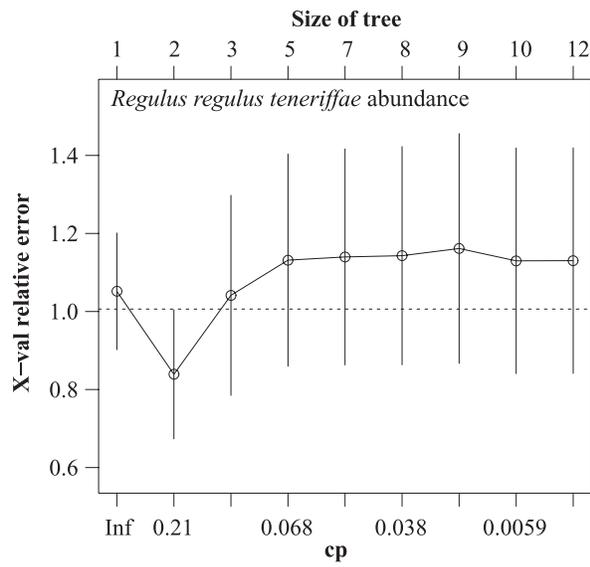


APPENDIX I. continued.



* a = first year of study, s = second year of study

APPENDIX I. continued.



APPENDIX I. continued.

