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Patterns of bird diversity and habitat use in mixed vineyard-matorral landscapes of Central Chile

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ABSTRACT

The Mediterranean climate region of central Chile is rich in biodiversity and contains highly productive agricultural lands, which creates challenges for the preservation of natural habitats and native biodiversity. Ecological data and studies for the region are also limited, making informed conservation in agricultural landscapes difficult. The increasing availability of remotely sensed data provide opportunities to relate species occurrences to measures of landscape heterogeneity even when field measures of habitat structure are lacking. When working with such remotely sensed data, it's important to select appropriate measures of heterogeneity, including common metrics of landscape composition as well as frequently overlooked shape metrics. In this contribution we combine bird surveys with multispectral satellite imagery to develop boosted regression tree models of avian species richness, and of habitat use for 15 species across a mixed vineyard-matorral landscape in central Chile. We found a range of associations between individual species and land cover types, with the majority of species occurring most frequently in remnant habitats and ecotones rather than the interiors of large vineyard blocks. Models identified both metrics of landscape composition and patch shape as being important predictors of species occurrence, suggesting that shape metrics can complement more commonly used metrics of landscape composition. Vineyards that include corridors or islands of remnant habitat among vine blocks may increase the amount of area available to many species, although some species may still require large tracts of intact natural habitat to persist.

1. Introduction

The coincidence of high levels of biodiversity in areas of dense human population and areas of high agricultural value is a well-studied phenomenon (Cincotta et al., 2000; Imhoff et al., 2004; Myers et al., 2000; Williams, 2013). In places where such overlap occurs, agricultural priorities often take precedence over conservation. Chile in particular, has had limited success in efforts to promote and incorporate conservation measures within the context of an agricultural sector that enjoys strong economic influence and policy support (Armesto et al., 2010; Budds, 2013; Carruthers, 2001; Valdes and Gnaegy, 1996). Even where conservation policies within agricultural areas are in place, the outcomes are mixed (Kleijn and Sutherland, 2003), as is the case in many of the world's Mediterranean-type ecosystems (Underwood et al., 2009).

Given this backdrop, it is valuable to consider how the design or restoration of agricultural landscapes can aid in supporting regional conservation strategies. Strategies such as the incorporation of hedgerows, riparian buffers, and/or the conservation of remnant vegetation patches may successfully provide adequate habitat for diverse species, especially when informed by a scientifically-based understanding of species-habitat relationships (Kremen et al., 2012; Perfecto and Vandermeer, 2008; Viers et al., 2013). While continued efforts to protect and set aside natural habitat will be critical for many conservation efforts, a complementary approach that focuses on mechanisms and incentives to achieve conservation

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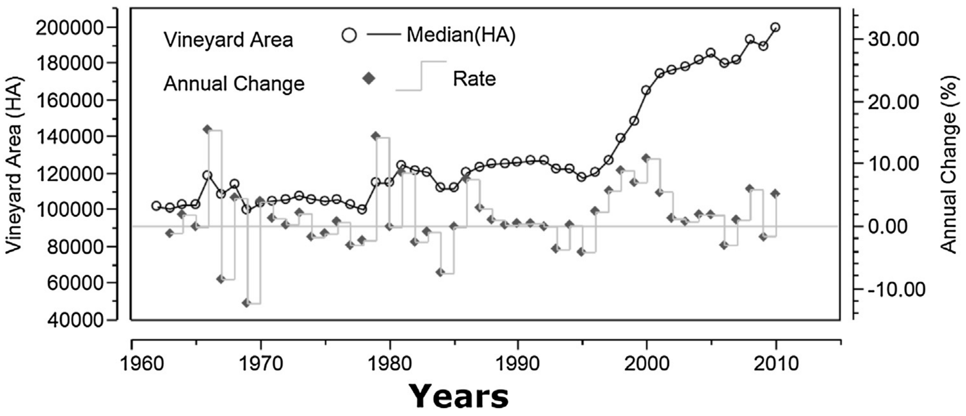

Fig. 1. Estimated vineyard footprint and trends for Chile between 1962 and 2010. Partial Figure from Viers et al., 2013 (Viers et al., 2013). Data sources: CWI (http://www.wineinstitute.org/files/WorldVineyardAcreagebyCountry.pdf); FAO (http://faostat.fao.org); OIV (http://www.oiv.int/oiv/info/frstatoivextracts2).

within the context of existing and expanding agricultural footprints is feasible and can also have broad impacts (Cox and Underwood, 2011; Rosenzweig, 2003). Identifying opportunities for conservation within agricultural landscapes is especially relevant to Chile's central valleys, where only 1–3% of the Mediterranean-type ecosystems (depending on how they are defined) fall within the National Protected Areas System (Cox and Underwood, 2011; Wilson et al., 2007). Among the dominant pressures on these ecosystems is the presence and continued expansion of vineyard plantations (Fig. 1), which fuel the country's thriving wine industry but also reduce the extent of matorral and sclerophyll forest habitats, reduce remnant patch size, and facilitate the spread of invasive species (Aguayo et al., 2009; Fuentes et al., 2013; Scherson et al., 2014).

There is a long history of ecological research demonstrating the correlation between habitat heterogeneity and animal species diversity (Tews et al., 2004a and citations therein), which has been extended both theoretically and empirically to agricultural systems (Bennett et al., 2006; Fahrig et al., 2011; Weibull et al., 2003). Remotely sensed imagery – which has become increasingly accessible and affordable – can be used to quantify heterogeneity of existing land cover, even in areas where there is limited field data. Through the use of flexible statistical analyses (e.g., boosted regression trees), one can model complex relationships between these agricultural landscape patterns and species occurrence information to develop spatially explicit habitat suitability models. In turn, these models can be used to predict how landscape features may affect biodiversity or individual species occurrences. These models can be especially valuable for conservation planning in areas where detailed biological data and ecological studies are scarce (Armstrong and McCarthy, 2007; Gossa et al., 2015).

Selecting appropriate metrics to describe the heterogeneity of a landscape is essential in leveraging remotely sensed data to create habitat suitability models, and in this case to ultimately inform efforts towards making vineyard landscapes more biodiversity-friendly. Often habitat heterogeneity is characterized by the number or variance of different habitat patches within a landscape (Tews et al., 2004a). Such metrics describe the composition of land cover types and are insensitive to spatial attributes such as patch shape. However, spatially explicit measures of landscape heterogeneity are also readily available (McGarigal et al., 2012) and may complement compositional metrics in describing wildlife diversity and habitat use (Schindler et al., 2013).

The aim of this paper is to examine the relative importance of spatially explicit shape metrics in describing the relationship between habitat heterogeneity, and both Chilean bird species richness and habitat use in a vineyard-dominated landscape. We also evaluate the utility of boosted regression trees for integrating a variety of landscape metrics to quantify species-habitat relationships from limited field data. We believe this approach can inform future research in agricultural areas, as well as provide useful insight and guidance for increased accommodation of biodiversity in working landscapes. This can be particularly important for areas such as Chile's Mediterranean region where agricultural development is proceeding rapidly, and where local research informing sustainable agriculture and conservation practices is sparse.

2. Methods

2.1. Study area

Study sites were located in the Colchagua Valley (34.68° S, 71.14° W), a recognized wine region in the sixth region of central Chile (Fig. 2). The climate is Mediterranean with warm, dry summers and cool, wet winters (Di Castri and Hajek, 1976). Chile's Mediterranean region makes up only 19% of the country's land area, and yet supports 77% of the human population and encompasses 39% of the area devoted to agriculture, grazing and timber (Barbosa and Villagra, 2015; Instituto Chileano Nacional de Estadisticas, 2007, 2011). We focused on three vineyards, all of which abut the undeveloped Rucatalca or Alto del Huique hills and thus contain a matrix of remnant and vineyard habitats within their properties. The vineyard management strategies of the three properties range from conventional (Montes – Apalta estate), to certified organic and biodynamic (Emiliana – Los Robles estate) with Caliterra's Colchagua estate containing both conventionally and organically managed vineyard blocks. All work was conducted on private property with the owners' approval. Surveys were non-invasive and no additional permitting or permissions were required.

2.2. Bird surveys

Avian point count surveys were conducted at 48 points within the three properties between September 27th and December 3rd, during the breeding season of 2011. Sites were stratified across three habitat categories: natural remnant (nine survey points in forest habitats and seven points in shrubland habitats), vineyard, and their ecotone (ecotone points were located within 50 m of the habitat boundary; Fig. 3). Each point was surveyed three times during the breeding season for bird species occurrence. At each point a 5-min survey was conducted, where an experienced observer identified as many individuals by sight or sound as possible (Ralph et al., 1995). Surveys were completed within four hours of sunrise when birds were most active. Points were located along transects and spaced at a minimum of 250 m apart. In surveys conducted

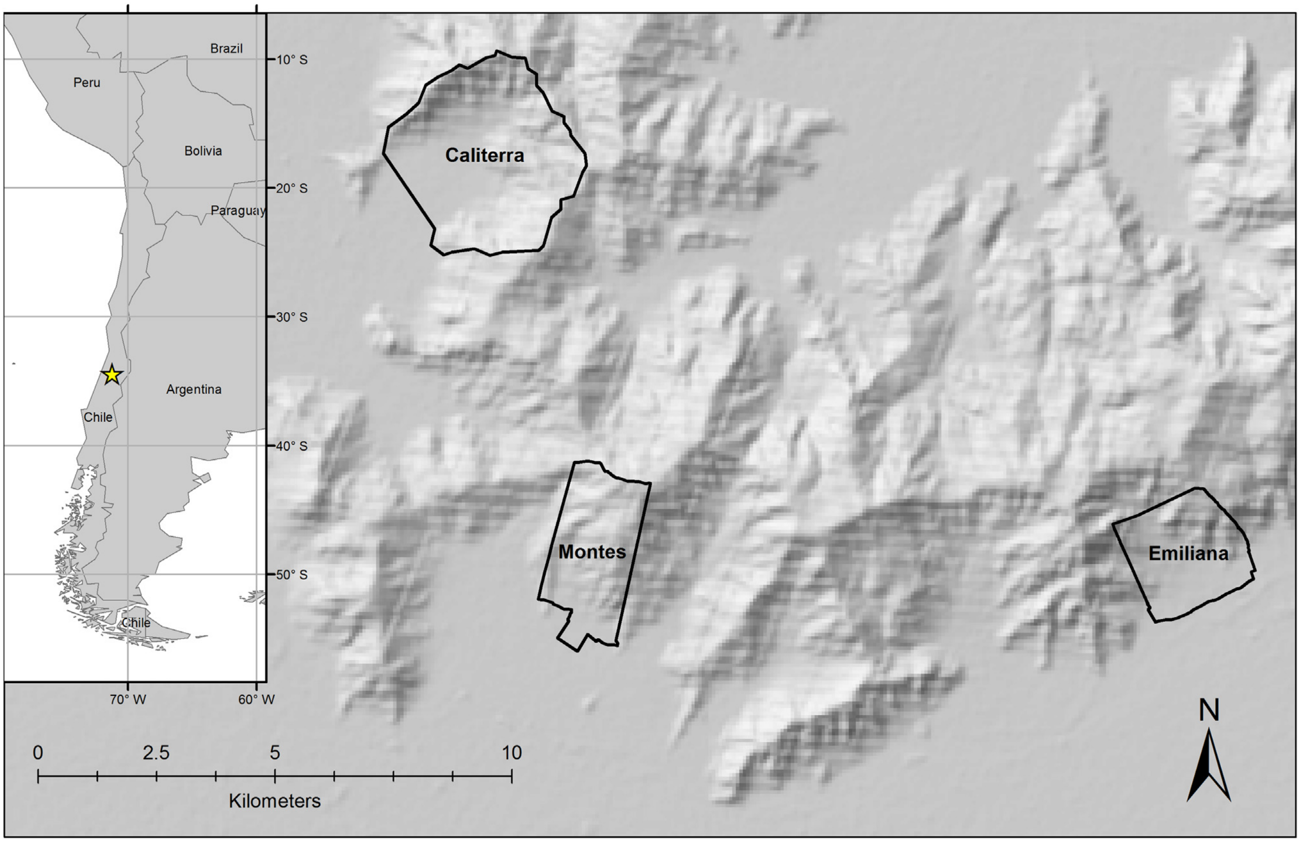

Fig. 2. Project study area. Approximate land area of the Caliterra, Montes and Emiliana estates are 1239, 611 and 524 ha respectively.

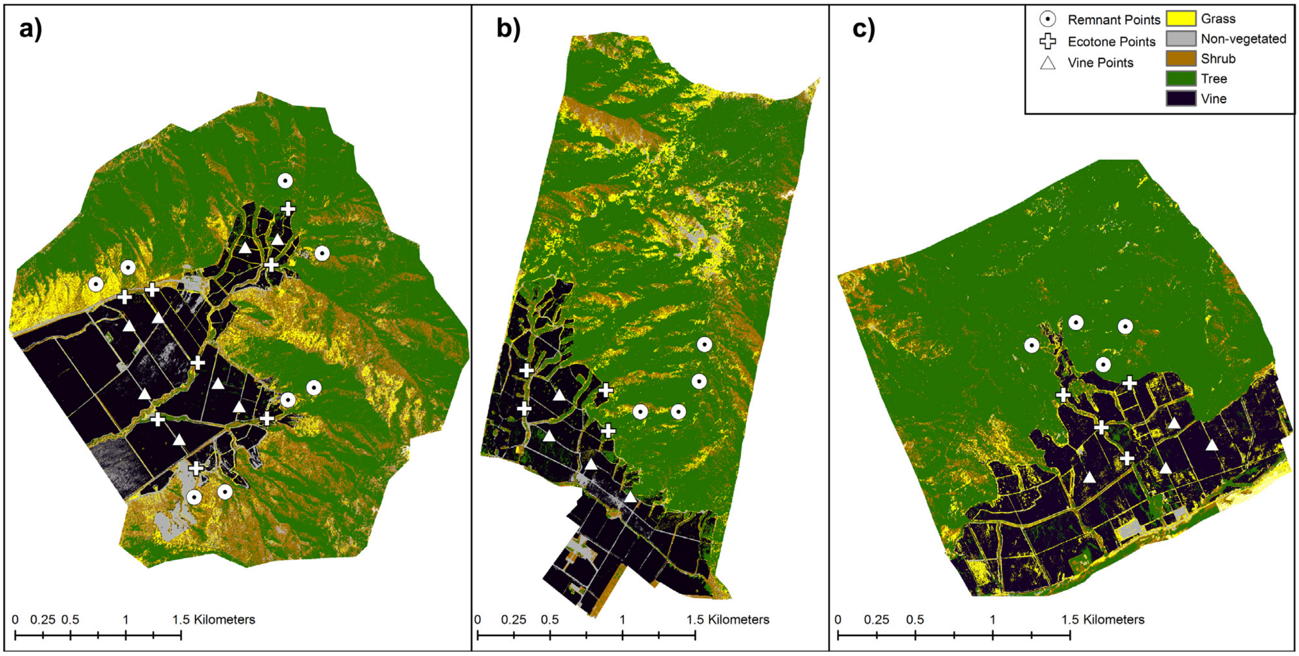

Fig. 3. Land cover classifications and bird survey locations. a) Caliterra, b) Montes and c) Emiliana vineyards. Ecotone points are within 50 m of habitat boundaries.

along natural/vineyard boundaries (ecotone points), the habitat type in which each individual bird was first observed was also noted. Species richness and Simpson's diversity were compared between habitat categories using ANOVA.

2.3. *Land cover classification & landscape metrics*

Eight-band World View 2 multispectral satellite imagery was used for all three vineyards. These images were orthorectified and a supervised classification procedure was conducted using ENVI version 4.8 (Exelis Visual Information Solutions, Boulder, Colorado) to

Table 1
Landscape predictor variables used in boosted regression tree models.

Metric	Description
Farm	Blocking metric accounting for unmeasured unique attributes of each property
Landscape Composition Metrics	
Pland	Landcover type as percent of landscape (%)
PR	Patch richness (number of patch types)
SHDI	Shannon diversity index (of patch types)
Patch Shape Metrics	
Contig[a]	Contiguity index – contiguous cover types have high values, fragmented types have low values
Complex[a,b]	Patch complexity – analogous to perimeter-area ratio, but standardized for patch size (range: 1–∞, from most simple to increasingly complex)
Circle[a]	Related circumscribing circle – measure of patch elongation as compared to a circle (range: 0–1, from a perfect circle to most elongated)

[a] Calculated as the area-weighted for each cover class.

[b] Known as “Shape” in Fragstats documentation; changed here to avoid confusion.

identify five land-cover classes: 1) shrub, 2) tree, 3) grass, 4) non-vegetated and 5) vine (Fig. 3). Classified surfaces were analyzed using Fragstats version 4.1 (McGarigal et al., 2012) to calculate various landscape metrics using a moving window procedure. This procedure calculates values for each pixel within the study area based on a circular window (local landscape) with a radius of 150m. Metrics were categorized as landscape composition metrics or patch shape metrics (Table 1).

Percent of landscape (Pland), contiguity index (Contig), patch complexity (Complex) and related circumscribing circle (Circle) metrics were evaluated for each of the five land cover classes. Shannon diversity index of patch types (SHDI) and patch richness (PR) were calculated across the local landscape as summaries of all land cover classes. Complete descriptions for fragstats-derived variables can be found at http://www.umass.edu/landeco/research/fragstats/fragstats.html

2.4. Model construction & evaluation

To evaluate landscape use, species presence/non-detection models were built using boosted regression trees (BRTs) with point count species data and landscape metrics calculated from satellite imagery. BRTs combine the two modeling techniques of 1) regression trees, where simple models are built relating predictive and response variables through recursive binary splits while ignoring non-informative predictors, and 2) boosting, where individual trees are combined adaptively based on residual deviance to improve predictive performance (Elith et al., 2008). Large regression trees are characterized by high variance and low bias (De'ath, 2007). By introducing stochasticity (through “bagging” or bootstrap aggregation) and by performing cross-validation (dividing the dataset for model training and validation), BRTs are able to achieve high levels of accuracy and reduce variance without over-fitting (De'ath, 2007). Among the advantages of BRTs are their high predictive performance relative to traditional modeling methods, ability to fit complex nonlinear relationships and interaction effects automatically, to accommodate missing data, and to handle relatively large numbers of potential predictors by ignoring non-informative variables (De'ath, 2007; Elith et al., 2008). BRTs also perform better under conditions of high multicollinearity as compared to common regression techniques (e.g., generalized linear models; Dormann et al., 2013). Nevertheless, we limited the number and redundancy of our predictor variables from the many available (McGarigal et al., 2012) in part to reduce multicollinearity. Of the limited set of candidate predictors used in our models, only 7% of pairwise correlations between predictors have an absolute value greater than 0.7 (correlation matrix in Appendix File C.3).

Use of BRTs for presence/non-detection prediction is a relatively new modeling technique in the field of ecology, but is being applied successfully for many focal taxa and to answer a variety of questions (e.g., Richards et al., 2012; Stralberg et al., 2015; Yang et al., 2016; Zhang et al., 2014). There are many advantages of BRTs over linear-model approaches, but one potential limitation is that BRTs do not explicitly account for imperfect detection. Imperfect detection is a known challenge when assessing the occurrence of mobile species and can lead to biased estimates of species richness and habitat occupancy (MacKenzie et al., 2003). We expect this to be a minor issue within the open vineyard habitats of this study, but rates of detection in the structurally more complex shrub and forest habitats may be somewhat lower. For common species, this could result in underestimates of occurrence within natural habitats, and some rare species that occur only in natural habitats may have been missed altogether. Thus, our estimates of occurrence and richness in natural areas should be viewed as conservative, and the contrasts between vineyard and natural habitats may in fact be larger than observed.

For our purposes, a species was considered present at a given point if it was observed within 50 m of the survey location during at least one of the three visits. BRT models constructed for individual species were run using a binomial error structure with presence/non-detection of a species at a given point as the response variable. Separately, a species richness BRT model was run using a Poisson error structure with number of species present at a site as the response variable. For each model, a custom optimization procedure was run to find the best combination of the following BRT meta-parameters (sensu Richards et al., 2012): bag fraction (0.5, 0.6, 0.7, 0.8, 0.9), tree complexity (1, 2, 3, 4, 5) and learning rate (0.05, 0.01, 0.001, 0.0001). The bag fraction specifies the proportion of data used in a bootstrapped sample to fit each individual tree, allowing for a level of stochasticity in the model building process. Tree complexity determines the degree to which interactions are fit in the model, as variables fit on subsequent branches of a tree are dependent on the variables fit higher on the tree hierarchy. The learning rate determines the contribution of each tree to the aggregated model, with slower learning rates reducing overfitting but increasing computation load (Elith et al., 2008).

During the optimization procedure, the deviance explained by each set of candidate meta-parameters, as estimated through 10-fold cross-validation, was used to identify the optimal set of meta-parameters. Because it is difficult to construct adequate species presence/non-detection models for rare or elusive species with few observed presences, we attempted to build models only for sixteen species that were observed at a minimum of ten survey points. For one of these sixteen species, the BRT algorithm did not converge, suggesting greater sample size and/or improved predic-

Table 2
The scientific name, English common name and 4-letter code used for all species for which a species presence/non-detection model was constructed. The species richness model was not limited to species listed here.

Scientific Name	English Common Name	4-letter Code[a]
Curaeus curaeus	Austral Blackbird	AUBL
Carduelis barbata	Black-chinned Siskin	BCSI
Phrygilus alaudinus	Band-tailed Sierra-finch	BTSF
Callipepla californica	California Quail	CAQU[b]
Mimus thenca	Chilean Mockingbird	CHMO
Nothoprocta perdicaria	Chilean Tinamou	CHTI
Pseudasthenes humicola	Dusky-tailed Canastero	DTCA
Xolmis pyrope	Fire-eyed Diucon	FEDI
Sicalis luteola	Grassland (Misto) Yellow-finch	GYFI
Troglodytes aedon	Southern House Wren	HOWR
Sturnella loyca	Long-tailed Meadowlark	LTME
Columbian picui	Picui Ground-dove	PGDO
Leptasthenura aegithaloides	Plain-mantled Tit-spinetail	PMTS
Anairetes parulus	Tufted-tit Tyrant	TTTY
Elaenia albiceps	White-crested Elaenia	WCEL

[a] Codes used follow the North American bird banding program convention.
[b] California Quail is a non-native species introduced from North America.

tor variables were needed. Thus we successfully modeled presence probabilities for 15 species, as well as for overall species richness, which includes all species observed during standardized surveys (Table 2).

Models were run using 10-fold cross-validation to allow for estimates of predictive performance. Model predictive performance was evaluated using two separate metrics: 1) the proportion of total deviance explained by the predictor variables, and 2) the area under the curve metric (AUC) of the receiver operating characteristic analysis. AUC is a measure of model goodness of fit where values close to 1 indicate that a model consistently identifies true presences whereas values near 0.5 indicate model predictions are no better than random (Fawcett, 2006). AUC values are not calculated for Poisson models, thus only the proportion of deviance explained was used when evaluating our richness model. The statistical program R (R Development Core Team, 2011) was used for all statistical analysis, and BRTs were developed using the gbm.step function in the *dismo* package (Hijmans et al., 2011).

3. Results

3.1. Bird surveys

A total of 36 bird species were identified within 50 m of the observer during standard survey periods. An additional 8 species were observed within the vineyard properties either between surveys or beyond our 50-m cut-off, and were not included in our analysis (Table A.1). Among the 36 surveyed species, one is introduced (California Quail – *Callipepla californica*) and five are endemic to Chile (Chilean Tinamou – *Nothoprocta perdicaria*, Dusky Tapaculo – *Scytalopus fuscus*, Dusky-tailed Canastero – *Pseudasthenes humicola*, Moustached Turca – *Pteroptochos megapodius*, and White-throated Tapaculo – *Scelorchilus albicollis*) (Jaramillo, 2003). The Chilean Tinamou was observed within vineyard habitats, but the other endemics were only encountered in remnant habitats. Chilean Tinamou and Dusky-tailed Canastero were the only endemic species observed frequently enough to model on an individual species basis.

ANOVA tests indicated a greater number of species was observed on average during surveys along ecotones (mean = 7.6; sd = 1.1) and within remnant habitat (mean = 6.6; sd = 1.4) than within vineyards (mean = 4.0; sd = 1.0; $F_{2,45} = 39.7$). Likewise, Simpson's diversity index was greater for ecotone (mean = 0.86; sd = 0.03) and remnant points (mean = 0.83; sd = 0.05) than for vineyard points (mean = 0.67; sd = 0.12; $F_{2,45} = 26.68$). Tukey's honestly significant difference test showed differences to be statistically significant ($p < 0.001$) between vineyards and sites with natural habitat (ecotone or remnant sites) for both richness and Simpson's diversity index. Between ecotone and remnant sites, species richness was marginally different ($p = 0.07$), and did not show a difference in Simpson's index ($p = 0.57$; Fig. 4).

3.2. Model optimization and performance

BRT models were successfully run for 15 individual species and for species richness with the optimal combination of parameters varying across models (Table 3). Models for species richness, Band-tailed Sierra-finch (BTSF), Plain-mantled Tit-spinetail (PMTS), and White-crested Elaenia (WCEL) performed best according to percent of total deviance explained with 51%, 36%, 35%, and 34%, respectively.

3.3. Predictor variables

BRT models assign a partial influence score (a percentage value of relative importance) to each predictor variable. This metric is based on the number of times each variable is selected when building individual regression trees and the relative improvement to the overall model as a result of its selection (Elith et al., 2008). To look at the importance of shape and composition in describing species occurrence and richness, we aggregated partial influence scores for each model by the variable groups outlined in Table 1. On average across the 16 models, shape variables make up the greatest percentage of influence (60%), followed by composition variables (37%), and the farm blocking variable (3%). The variable group comprising the greatest percentage of influence varies across individual models (Fig. 5), but shape variables are most important in fourteen of the sixteen models, with only the Dusky-tailed Canastero and Southern House Wren models attributing more than 50% of the relative influence to composition variables (Fig. 5; Table 4).

On average, the individual variables of percent area planted in vines, and Circle (a shape measure of patch elongation as compared to a circle) for the vine cover type were the most influential across the 16 models assessed with an average of 13% and 12%, respectively. These variables were followed by contiguity of trees, the complexity of vine patches, and the percent area covered by trees (Table 4). No single variable was selected as most important across all models. Six variables were identified as the most important more than once.

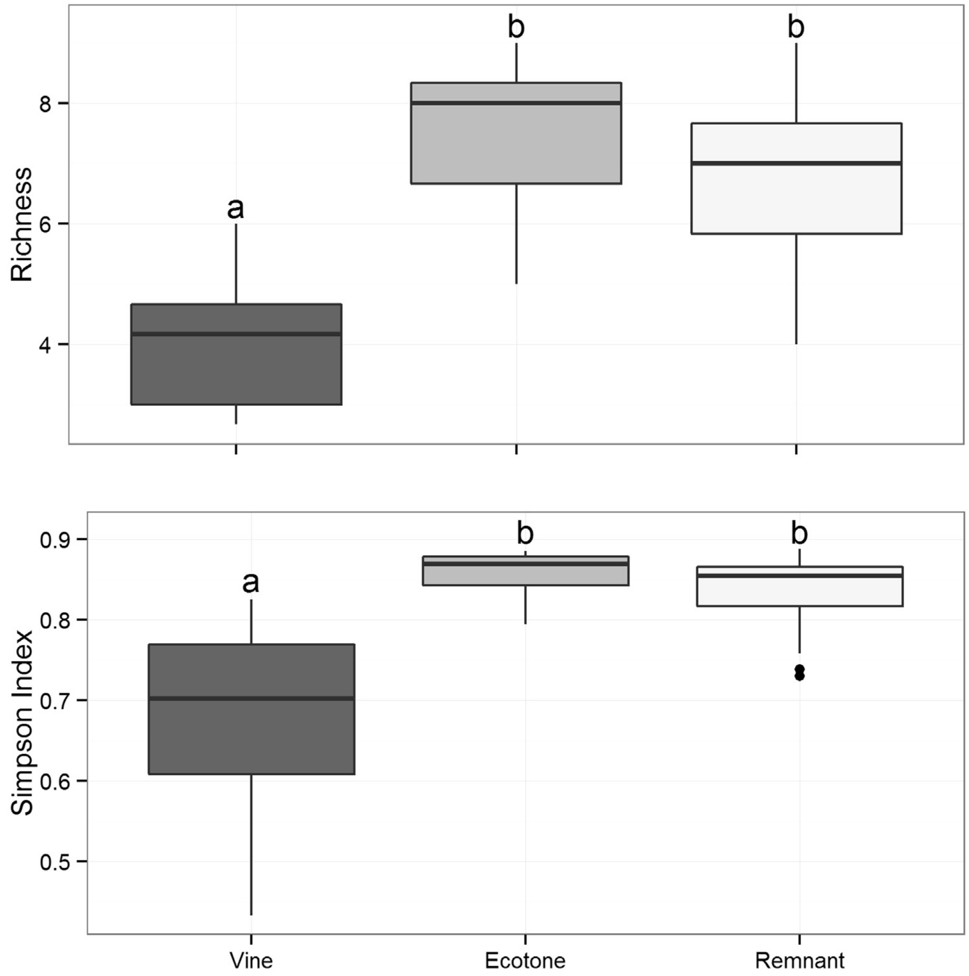

Fig. 4. Boxplots of bird species diversity among three habitat types across a vineyard-natural landscape in central Chile. N = 16 for each category with each datum representing the mean across three return visits. Boxplots with different letters are significantly different at $p < 0.001$. The difference in richness between ecotone and remnant points was marginally significant at $p = 0.07$.

Table 3
Optimized boosted regression tree model parameters and model performance measures for the 16 models evaluated. Models are sorted by percent deviance explained.

	Optimal parameters				Model performance[a]		
Model	Tree Complexity	Learning Rate	Bag Fraction	# of Trees	CV AUC – Mean	CV AUC – SE	Deviance Explained (%)
Richness	5	0.01	0.9	550	NA	NA	51
Band-tailed Sierra-finch	3	0.001	0.6	3600	0.90	0.06	36
Plain-mantled Tit-spinetail	1	0.01	0.9	300	0.91	0.05	35
White-crested Elaenia	2	0.001	0.6	4500	0.91	0.03	34
Southern House Wren	2	0.01	0.9	2400	0.85	0.06	28
Dusky-tailed Canastero	2	0.01	0.5	200	0.83	0.06	22
Long-tailed Meadowlark	1	0.01	0.5	200	0.72	0.05	18
Tufted-tit Tyrant	4	0.001	0.6	2600	0.72	0.09	17
Picui Ground-dove	3	0.001	0.6	2200	0.76	0.08	17
Chilean Mockingbird	5	0.01	0.7	300	0.74	0.08	12
Austral Blackbird	3	0.001	0.8	1000	0.75	0.07	8
California Quail	1	0.01	0.9	200	0.69	0.06	7
Grassland Yellow-finch	1	0.01	0.6	250	0.69	0.09	6
Chilean Tinamou	5	0.001	0.9	2450	0.68	0.10	6
Fire-eyed Diucon	4	0.01	0.5	200	0.62	0.06	4
Black-chinned Siskin	4	0.001	0.6	900	0.58	0.06	3

[a] CV = Cross Validation. AUC = Area Under the Curve of the receiver operating characteristic. AUC values are calculated for binomial models only, thus are not included for the species richness model.

Partial influence plots of the four most influential predictor variables are presented in Fig. 6 for the four highest performing models, as measured by percent of total deviance explained (Table 3; see Appendix Fig. B.1 for plots of the remaining 12 models). For the species richness model, the shape of vine patches as they relate to a circle (Circle variable) and percent area in vine were the most important variables, accounting for 33.2% and 21.4% of the variation respectively (Fig. 6a). The marginal effect of the shape variable Cir-

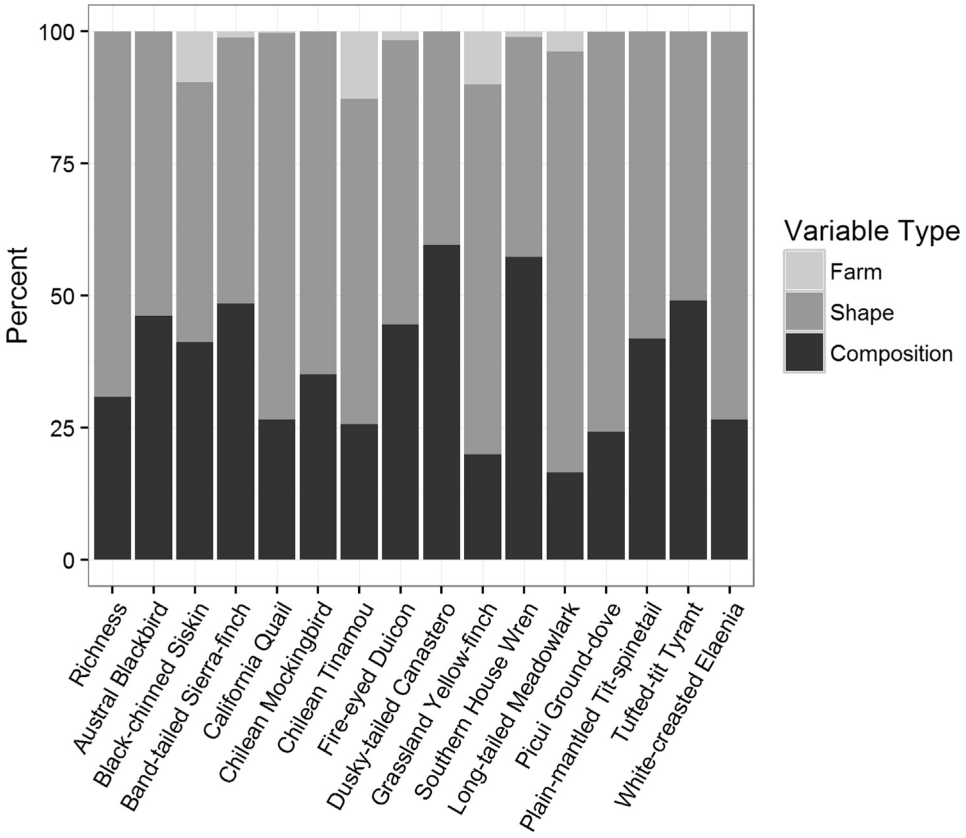

Fig. 5. Relative influence scores as aggregated by variable type. Composition metrics include percent area of each cover type, cover type richness, and Shannon diversity index of cover types. Shape metrics include contiguity index, a measure of patch complexity (Complex), and a measure of elongation (Circle). Farm is a blocking variable for survey location. Full variable descriptions are in Table 1.

Table 4
Relative influence (%) of the 10 most influential variables on average, grouped by metric type across all models regardless of effect directionality. The most important variable for each model is in bold text. Variable descriptions can be found in Table 1.

Model	Composition					Shape				
	Pland – vines	Pland – trees	SHDI	Pland – shrubs	Pland – Unvegetated	Circle – vines	Contig – trees	Complex – vines	Complex – shrubs	Contig – grass
Richness	21	1	6		1	**33**	1	9	1	4
Austral Blackbird	3	23	19		1	**39**	1	8		
Black-chinned Siskin			1	1	**23**	1	11	6	1	1
Band-tailed Sierra-finch	21	**26**			1	1	15	2	1	6
California Quail	1	15	10			18	7	**22**	17	1
Chilean Mockingbird	2	1	**26**	4	1	8	1	5	7	18
Chilean Tinamou	5		2	**16**	1	14		10	1	
Fire-eyed Diucon	10	1	**16**	5	8	3	4	6	5	4
Dusky-tailed Canastero	**40**	9	1	6	2	9	1	2	5	3
Grassland Yellow-finch	1		9	2	6	9	1	**25**	3	
Southern House Wren	**40**	1		14	1	24		5		1
Long-tailed Meadowlark	3	4	1	1	7	2	**45**	1	1	2
Picui Ground-dove		5	13	1	5	2	5	16	**17**	5
Plain-mantled Tit-spinetail	42					1	**44**	2	6	3
Tufted-tit Tyrant	8	**26**		12		1	4	5	1	3
White-crested Elaenia	13			12		**32**	8	13	1	5
Mean	13	7	7	5	3	12	9	8	4	4

cle was negative at low values (highly circular patches) but positive at high values (highly elongated patches). The number of expected species declines when more than approximately 75% of the area within 150 m is composed of vines (Fig. 6a). Together, these two marginal effects imply species richness is low when the majority of the local landscape is covered in vines, but that irregular elongated patches of vine promote higher diversity than compact patches.

The individual species models illustrate distinct species-habitat associations, likely due to differential natural history strategies. For example, the model of Band-tailed Sierra-finch (BTSF; Fig. 6b) shows a positive marginal effect when the percent area in trees is less than 15% and when over 50% is planted in vines. To a lesser extent, the BTSF model suggests a negative association with contiguity of trees and a positive association with the contiguity of shrubs. In contrast to BTSF, partial influence plots for both the Plain-

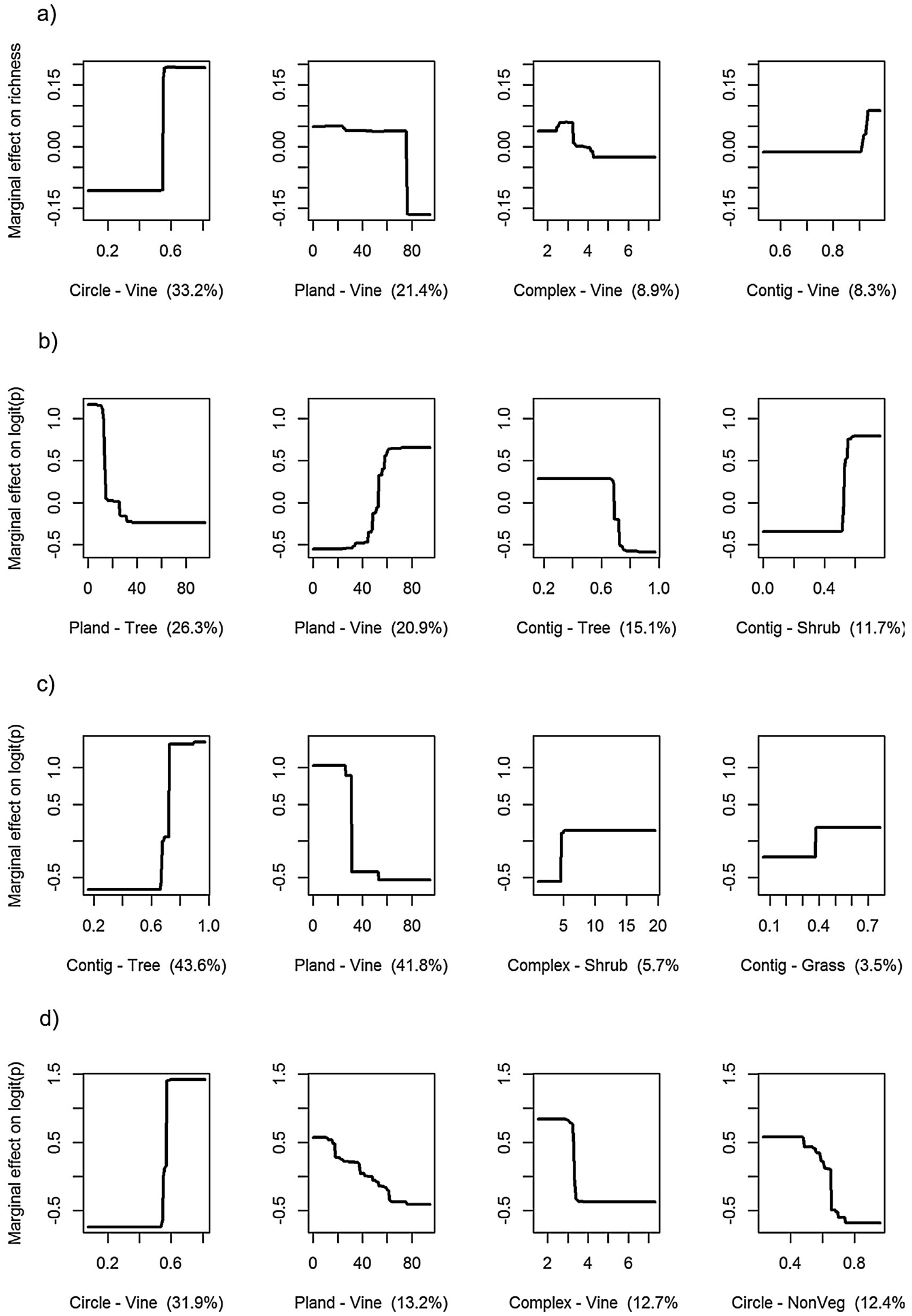

Fig. 6. Model partial influence plots. Plots display the four most influential predictor variables for the a) species richness, b) Band-tailed Sierra-finch, c) Plain-mantled Tit-spinetail, and d) White-crested Elaenia. Percentages indicate the relative influence of each variable on the response. Variable abbreviations are defined in Table 1.

mantled Tit-spinetail (PMTS; Fig. 6c), and White-crested Elaenia (WCEL; Fig. 6d) show negative associations with percent area in vines. However, the most important association for the PMTS model is an increased likelihood of presence when contiguity of trees is high. The PMTS model also shows a slightly increased likelihood of presence with more complex shrub patches, and more contiguous grass patches. The WCEL model shows a strong increase in likelihood when vine patches are elongated (high Circle value), and a decreased likelihood as vine complexity increases and as non-vegetated areas become more elongated.

4. Discussion

A sound understanding of the relationships between biodiversity and landscape features in human-dominated systems is needed to mitigate impacts of existing and future agricultural development. In this study, we found that combining field-based diversity measures with remotely-sensed measures of land use helped identify places where diversity and landscape structure are complementary. We found that while measures of compositional diversity of habitat are important (Tews et al., 2004c), the shape of habitat patches is particularly useful for predicting the suitability of a landscape for both individual species and bird diversity in general.

The results show a pattern of higher bird species diversity in ecotone and remnant matorral habitat relative to vineyard blocks (Figs. 4 & 7 a), which conforms to the general ecological understanding that most species prefer complex natural vegetation to simplified crop fields (e.g., Harvey and Villalobos, 2007; Puckett et al., 2009). Specifically, the data and model predictions presented in this study suggest that the effective habitat value for many bird species (although certainly not all) is higher when landscape configurations maintain a substantial component of non-vineyard habitats. Thus, existing vineyards should strive to integrate more ecotones, and if new vineyard blocks are to be planted, that they are done so in elongated rather than compact shapes and maximize ecotones while minimizing conversion of intact habitat. It is important to note that we consider the potential species diversity benefits of increased ecotones relative to agricultural land with no adjoining natural habitat. It is unlikely that increasing habitat edge under other conditions (e.g., through fragmentation or reduction of intact natural habitat) will increase the conservation value of land generally (Baker et al., 2002; Zipkin et al., 2009). Even in cases where diversity increases by allowing forest and shrubland specialists to coexist with generalist species, the benefits to generalist species may come at the expense of increased long-term risk to sensitive specialists (Flaspohler et al., 2001).

4.1. Relevant landscape metrics

Our models showed both landscape composition and shape metrics to be strongly related to avian habitat use. The percent area in vines (a composition metric) had the highest mean relative influence. More species are expected when vines are not the dominant cover type relative to native vegetation, and the likelihood of presence of the Dusky-tailed Canastero, Plain-mantled Tit-spinetail, Southern House Wren, and White-crested Elaenia decreases with increased vine cover. In contrast to this general prediction, two species, the Fire-eyed Diucon and Band-tailed Sierra-finch, showed positive associations with high levels of vine cover.

The shape metric that measured the elongation of vine patches had nearly as strong of an influence as the area of vines. A greater number of species along with a higher likelihood of individual species presence are expected when vineyard blocks are elongated rather than circular. Not only does this configuration increase the amount of edge habitat, but it also decreases the minimum distance that an individual must travel to cross a vineyard patch—a potentially important feature for those species that consider vines as an inhospitable matrix between habitat patches. Birds who favored elongated relative to circular patches included Austral Blackbird, California Quail, Chilean Tinamou, Southern House Wren, and White-crested Elaenia, (Figs. 6 and B.1).

Taken together, these results suggest that many species avoid large circular patches of vines with little edge (ecotone) habitat, but may be tolerant of small, elongated, or fragmented vineyard blocks if incorporated with a diversity of other habitat types. These findings support previous studies from other agroecological systems that found greater bird diversity within adjacent non-crop habitat or along crop field edges (Best et al., 1995; Puckett et al., 2009). Based on these estimated associations, the models suggest that vineyard configurations that reduce the area of vine patches and increase edge density through the use of corridors or islands of natural vegetation likely provide higher habitat value for a greater number of species compared to extensive monocultures of vines with few or no natural vegetation features.

4.2. Common vs. rare and endemic species

Among the common bird species assessed individually, the three highest performing models predict non-uniform habitat preferences. The Band-tailed Sierra-finch (BTSF) model predicts presence only within core areas of large vineyard blocks, with low probability of presence among non-vineyard vegetation (Fig. 7b). In unaltered landscapes, BTSF is associated with shrubby sites near grassy patches (Jaramillo, 2003), which are perhaps mimicked by the shrub-like rows of vines and grassy inter-row spaces. By contrast, the Plain-mantled Tit-spinetail (PMTS) model predicted the species to occur virtually exclusively in areas outside of the vineyard footprint, even shunning vineyard edges or areas where remnant habitat remains intermixed with vineyard blocks (Fig. 7c). And while the PMTS was not common within the vineyards of this study (1 observation at a vineyard point), the PMTS is nevertheless found in a variety of habitats in central Chile including forests and matorral (Jaramillo, 2003). The White-crested Elaenia model produces predictions similar to the PMTS model with greater probability of presence assigned to areas where little vineyard exists (Fig. 7d). WCEL is a common forest species that is also found in a variety of non-forest habitats if trees or tall shrubs are present (Jaramillo, 2003). Thus, vineyard landscapes are likely to accommodate WCEL only when trees or larger patches of natural habitat remain amongst the vines.

Due to limited observations of less common species, we were not able to create presence/non-detection models for all bird species observed in this study. We can nevertheless use the sparse existing data to form preliminary conclusions and hypotheses about habitat use by rare species as a group. With the exception of the Chilean Tinamou, endemic species were exclusively observed in remnant areas (Fig. 8). Likewise our model of the Dusky-tailed Canastero showed a strong negative association with vineyards (Figs. B.1 & B.2). These observations suggest that vineyard cultivation may not be compatible with certain rare species of conservation interest in Chile and that intact natural habitat is likely necessary for their persistence, although more targeted and/or extensive surveys are needed.

4.3. Management implications

These findings show that avian habitat quality is heterogeneous across Chile's vineyard landscapes, and suggest ways in which vineyards can better accommodate biodiversity. Our study is limited to a single season of bird surveys within Chile's Colchagua Valley. We contend that even sparse data is valuable to conservation management due to the current scarcity of studies in this region, and that our approach may be applied in analogous studies for other agricultural systems. However, generalizations of our findings to other regions should be done only with consideration of complimentary studies. For example, similar to our findings that avian diversity is highest within natural habitats and ecotones, studies in different crop systems have found that while some woodland bird species will forage up to 200 m from a crop field edge, they are typically concentrated within 20–50 m of adjacent habitat (Best et al., 1990; Puckett et al., 2009). Additional work has shown that local land-cover heterogeneity, such as that found at ecotones, is

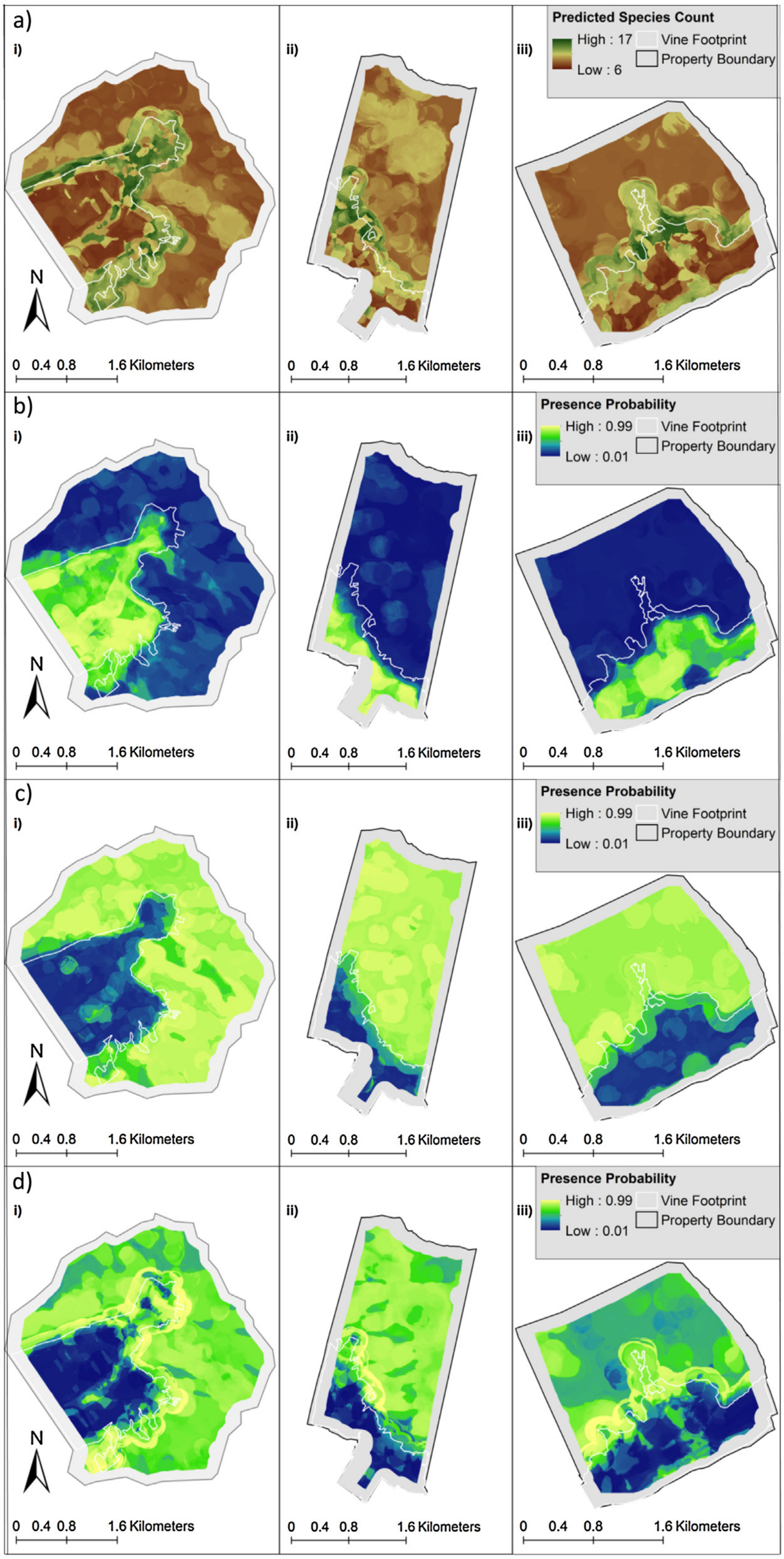

Fig. 7. BRT model predictions for the four top performing models mapped across the three farms sampled. Predictive species number or probability of presence for a) species richness, b) Band-tailed Sierra-finch, c) Plain-mantled Tit-spinetail, and d) White-crested Elaenia for the i) Caliterra, ii) Montes, and iii) Emiliana vineyards. Predictive maps for the additional 12 species can be found in Fig. B.2.

often positively correlated with species abundance (Quinn et al., 2014). Therefore, conservation management actions focused near cropland edges may be most efficient at increasing overall habitat quality.

Increasing non-cropland habitat and utilizing conservation-friendly practices within existing vineyard landscapes can also provide a number of co-benefits for agriculture (Rosenzweig, 2003; Smith et al., 2013), such as reduced wind erosion (Brandle et al.,

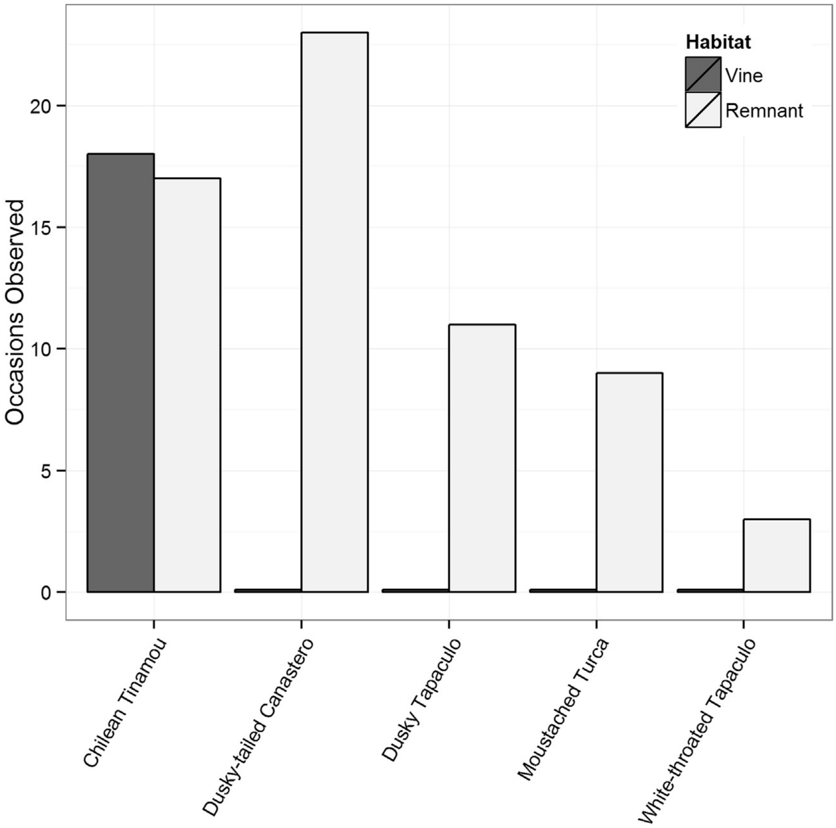

Fig. 8. Total number of observations of endemic species in vineyard vs. remnant habitats across all surveys. Dusky Tapaculo, Moustached Turca, and White-throated Tapaculo did not meet our modeling criteria of a minimum of ten survey points with at least one observation.

2004), improved water quality (Dosskey, 2001), increased carbon sequestration (Williams et al., 2011), and the suppression of crop pests via the enhancement of natural predators (Bianchi et al., 2006). There is the potential that increasing non-crop vegetation may harm grape yields via the encouragement of bird species that directly consume or damage fruit (Somers and Morris, 2002), although such concerns do not appear as prevalent in Chile's wine regions as elsewhere. In some cases, conservation efforts themselves can help reduce this risk, for example by encouraging natural predators of pest species (Kross et al., 2012). Ultimately, the relative benefits and costs of conservation actions will necessarily depend on local conditions and objectives.

Achieving conservation goals in mixed agricultural landscapes will require looking beyond the configuration of existing vineyards. For species that show poor compatibility with disturbed or altered habitat, such as the rare endemic bird species detected in this study, broader-scale protection of natural habitat and prevention of further agricultural expansion through land-acquisition, and preservation of adjacent undeveloped areas is likely needed (Hannah et al., 2013).

Research activities cannot be conducted in isolation from applied conservation. Successful integration of conservation measures into working landscapes will depend in part on the incorporation of findings such as ours into conservation and agricultural management. As such, research findings that increase our understanding of the interactions between biodiversity and vineyard landscapes must be communicated to managers and landowners in a manner that can be readily incorporated into existing business practices and are accessible to broad constituencies (Viers et al., 2013). Two successful examples of on-going collaborations in vineyard landscapes are the Wine, Climate Change and Biodiversity program (http://www.vccb.cl) in Chile and the Biodiversity and Wine Initiative in South Africa (http://wwf.org.za/bwi), which incorporate private, scientific and policy stakeholders in addressing conservation challenges. Additionally, recent investigations into winegrower behavior and perception have underscored the importance/usefulness of peer-to-peer networks in adopting sustainability practices (Lubell et al., 2011). Such communication and skills-sharing networks will be increasingly important for engaging growers at a personal level for reconciling winegrowing practices with biodiversity conservation (Nicholas and Durham, 2012).

5. Conclusions

Our findings support the general understanding that increasing conservation value within vineyard landscapes may effectively support some species, but likely not all. Within existing vineyards, increasing heterogeneity of habitat types and modifying vineyard block shape to create greater ecotone area are two approaches with predicted conservation benefits. However, any species that requires large, intact natural areas will be vulnerable to vineyard development, regardless of mitigating practices or vineyard design. For sensitive species, such as Chile's rare endemics, more intensive survey techniques are needed to fully understand how much and what characteristics of natural habitat are necessary for their preservation. Meanwhile, using remote sensing imagery to describe habitat heterogeneity, while considering both landscape composition and patch shape metrics, can be a useful tool for quantifying the present or potential conservation value of working landscapes. This combined approach can aid in the incorporation of conservation-minded strategies into vineyard and/or other agricultural crop management, encouraging practices and designs that have the potential to increase the area effectively available to many wildlife species.

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Appendices A–C. Supplementary data

Appendix A – tables, Appendix B – figures, Appendix C – data files associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.09.039.

References

Aguayo, M., Pauchard, A., Azocar, G., Parra, O., 2009. Land use change in the south central Chile at the end of the 20(th) century: understanding the spatio-temporal dynamics of the landscape. Revista Chilena De Historia Natural 82, 361–374.

Armesto, J.J., Manuschevich, D., Mora, A., Smith-Ramirez, C., Rozzi, R., Abarzua, A.M., Marquet, P.A., 2010. From the Holocene to the Anthropocene: a historical framework for land cover change in southwestern South America in the past 15,000 years. Land Use Policy 27, 148–160.

Armstrong, D.P., McCarthy, M.A., 2007. Big decisions and sparse data: adapting scientific publishing to the needs of practical conservation. Avian Conserv. Ecol. 2, 5.

Baker, J., French, K., Whelan, R.J., 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology 83, 3048–3059.

Barbosa, O., Villagra, P., 2015. Socio-ecological studies in urban and rural ecosystems in Chile. In: Rozzi, R., Chapin, F.S., Callicott, J.B., Pickett, S.T.A., Power, M.E., Armesto, J.J., May, R.H. (Eds.), Earth Stewardship: Linking Ecology and Ethics in Theory and Practice. Springer International Publishing, pp. 297–311.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biol. Conserv. 133, 250–264.

Best, L.B., Whitmore, R.C., Booth, G.M., 1990. Use of cornfields by birds during the breeding-season – the importance of edge habitat. Am. Midl. Nat. 123, 84–99.

Best, L.B., Freemark, K.E., Dinsmore, J.J., Camp, M., 1995. A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. Am. Midl. Nat. 134, 1–29.

Bianchi, F., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B Biol. Sci. 273, 1715–1727.

Brandle, J.R., Hodges, L., Zhou, X.H., 2004. Windbreaks in north american agricultural systems. Agrofor. Syst. 61–62, 65–78.

Budds, J., 2013. Water, power, and the production of neoliberalism in Chile: 1973–2005. Environ. Plan. D Soc. Space 31, 301–318.

Carruthers, D., 2001. Environmental politics in Chile: legacies of dictatorship and democracy. Third World Q. 22, 343–358.

Cincotta, R.P., Wisnewski, J., Engelman, R., 2000. Human population in the biodiversity hotspots. Nature 404, 990–992.

Cox, R.L., Underwood, E.C., 2011. The importance of conserving biodiversity outside of protected areas in Mediterranean ecosystems. PLoS One 6.

De'ath, G., 2007. Boosted trees for ecological modeling and prediction. Ecology 88, 243–251.

Di Castri, F., Hajek, E.R., 1976. Bioclimatologia de Chile. Universidad Catolica de Chile, Santiago, Chile.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Lafourcade, B., Leitao, P.J., Munkemuller, T., McClean, C., Osborne, P.E., Reineking, B., Schroder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.

Dosskey, M.G., 2001. Toward quantifying water pollution abatement in response to installing buffers on crop land. Environ. Manage. 28, 577–598.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112.

Fawcett, T., 2006. An introduction to ROC analysis. Pattern Recognit. Lett. 27, 861–874.

Flaspohler, D.J., Temple, S.A., Rosenfield, R.N., 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecol. Appl. 11, 32–46.

Fuentes, N., Pauchard, A., Sanchez, P., Esquivel, J., Marticorena, A., 2013. A new comprehensive database of alien plant species in Chile based on herbarium records. Biol. Invasions 15, 847–858.

Gossa, C., Fisher, M., Milner-Gulland, E.J., 2015. The research-implementation gap: howpractitioners and researchers from developing countries perceive the role of peer-reviewed literature in conservation science. Oryx 49, 80–87.

Hannah, L., Roehrdanz, P.R., Ikegami, M., Shepard, A.V., Shaw, M.R., Tabor, G., Zhi, L., Marquet, P.A., Hijmans, R.J., 2013. Climate change, wine, and conservation. Proc. Natl. Acad. Sci. U. S. A. 110, 6907–6912.

Harvey, C.A., Villalobos, J.A.G., 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodivers. Conserv. 16, 2257–2292.

Hijmans, R.J., Phillips, S., Leathwick, J.R., Elith, J., 2011. Package 'dismo'. R Package version 1.1.

Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R., Lawrence, W.T., 2004. Global patterns in human consumption of net primary production. Nature 429, 870–873.

Instituto Chileano Nacional de Estadisticas, 2007. VII censo agropecuario.

Instituto Chileano Nacional de Estadisticas, 2011. Estadisticas Demograficas, Compendio Estadistico.

Jaramillo, A., 2003. Birds of Chile. Princeton University Press Princeton and Oxford, New Jersey, USA.

Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40, 947–969.

Kremen, C., Iles, A., Bacon, C., 2012. Diversified farming systems: an agroecological, aystems-based alternative to modern industrial agriculture. Ecol. Soc. 17.

Kross, S.M., Tylianakis, J.M., Nelson, X.J., 2012. Effects of introducing threatened falcons into vineyards on abundance of passeriformes and bird damage to grapes. Conserv. Biol. 26, 142–149.

Lubell, M., Hillis, V., Hoffman, M., 2011. Innovation, cooperation, and the perceived benefits and costs of sustainable agriculture practices. Ecol. Soc. 16, 12.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84, 2200–2207.

McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continous Maps. University of Massachusetts, Amherst.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature (London) 403, 853–858.

Nicholas, K.A., Durham, W.H., 2012. Farm-scale adaptation and vulnerability to environmental stresses: insights from winegrowing in Northern California. Glob. Environ. Change Hum. Policy Dimens. 22, 483–494.

Perfecto, I., Vandermeer, J., 2008. Biodiversity conservation in tropical agroecosystems—a new conservation paradigm. Year Ecol. Conserv. Biol. 2008 (1134), 173–200.

Puckett, H.L., Brandle, J.R., Johnson, R.J., Blankenship, E.E., 2009. Avian foraging patterns in crop field edges adjacent to woody habitat. Agric. Ecosyst. Environ. 131, 9–15.

Quinn, J.E., Johnson, R.J., Brandle, J.R., 2014. Identifying opportunities for conservation embedded in cropland anthromes. Landsc. Ecol. 29, 1811–1819.

R Development Core Team, 2011. R: A language and environment for statistical computing, Vienna, Austria.

Ralph, C.J., Droege, S., Sauer, J.R., 1995. Managing and monitoring birds using point counts: standards and applicaitons. In: Ralph, C.J., Sauer, J.R., Droege, S. (Eds.), Monitoring Bird Populations by Point Counts. USDA Forest Service, Gen. Tech. Rep. PSW-GTR-149, Albany CA.

Richards, B.L., Williams, I.D., Vetter, O.J., Williams, G.J., 2012. Environmental factors affecting large-bodied coral reef fish assemblages in the Mariana Archipelago. PLoS One 7, 25.

Rosenzweig, M.L., 2003. Reconciliation ecology and the future of species diversity. Oryx 37, 194–205.

Scherson, R.A., Albornoz, A.A., Moreira-Munoz, A.S., Urbina-Casanova, R., 2014. Endemicity and evolutionary value: a study of Chilean endemic vascular plant genera. Ecol. Evol. 4, 806–816.

Schindler, S., von Wehrden, H., Poirazidis, K., Wrbka, T., Kati, V., 2013. Multiscale performance of landscape metrics as indicators of species richness of plants, insects and vertebrates. Ecol. Indic. 31, 41–48.

Smith, J., Pearce, B.D., Wolfe, M.S., 2013. Reconciling productivity with protection of the environment: is temperate agroforestry the answer? Renew. Agric. Food Syst. 28, 80–92.

Somers, C.M., Morris, R.D., 2002. Birds and wine grapes: foraging activity causes small-scale damage patterns in single vineyards. J. Appl. Ecol. 39, 511–523.

Stralberg, D., Matsuoka, S.M., Hamann, A., Bayne, E.M., Solymos, P., Schmiegelow, F.K.A., Wang, X., Cumming, S.G., Song, S.J., 2015. Projecting boreal bird responses to climate change: the signal exceeds the noise. Ecol. Appl. 25, 52–69.

Tews, J., Brose, U., Grimm, V., Tielboerger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004a. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004c. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the mediterranean biome. Divers. Distrib. 15, 188–197.

Valdes, A., Gnaegy, S., 1996. Economy-wide reform and agricultural recovery: observations of economic Darwinism among transition economies. Agric. Econ. 14, 143–157.

Viers, J.H., Williams, J.N., Nicholas, K.A., Barbosa, O., Kotze, I., Spence, L., Webb, L.B., Merenlender, A., Reynolds, M., 2013. Vinecology: pairing wine with nature. Conserv. Lett. 6, 287–299.

Weibull, A.C., Ostman, O., Granqvist, A., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodivers. Conserv. 12, 1335–1355.

Williams, J.N., Hollander, A.D., O'Geen, A.T., Thrupp, L.A., Hanifin, R., Steenwerth, K., McGourty, G., Jackson, L.E., 2011. Assessment of carbon in woody plants and soil across a vineyard-woodland landscape. Carbon Balance Manage. 6, 11.

Williams, J.N., 2013. Humans and biodiversity: population and demographic trends in the hotspots. Popul. Environ. 34, 510–523.

Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R., Possingham, H.P., 2007. Conserving biodiversity efficiently: what to do, where, and when. PLoS Biol. 5, 1850–1861.

Yang, R.M., Zhang, G.L., Liu, F., Lu, Y.Y., Yang, F., Yang, F., Yang, M., Zhao, Y.G., Li, D.C., 2016. Comparison of boosted regression tree and random forest models for mapping topsoil organic carbon concentration in an alpine ecosystem. Ecol. Indic. 60, 870–878.

Zhang, Y., Chen, H.Y.H., Taylor, A., 2014. Multiple drivers of plant diversity in forest ecosystems. Glob. Ecol. Biogeogr. 23, 885–893.

Zipkin, E.F., Dewan, A., Royle, J.A., 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. J. Appl. Ecol. 46, 815–822.