Original research article

Landscape composition influences abundance patterns and habitat use of three ungulate species in fragmented secondary deciduous tropical forests, Mexico

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HIGHLIGHTS

- Secondary ecosystems near forest fragments offer important resources for ungulates.
- Landscape composition influences ungulate abundance and presence.
- Anthropogenic variables predominantly affected Sign Encounter Rate of ungulates.
- Future abundance of ungulate populations is linked to local decisions for land use change.

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ABSTRACT

Secondary forests are extensive in the tropics. Currently, these plant communities are the available habitats for wildlife and in the future they will possibly be some of the most wide-spread ecosystems world-wide. To understand the potential role of secondary forests for wildlife conservation, three ungulate species were studied: *Mazama temama, Odocoileus virginianus* and *Pecari tajacu*. We analyzed their relative abundance and habitat use at two spatial scales: (1) Local, where three different successional stages of tropical deciduous forest were compared, and (2) Landscape, where available habitats were compared in terms of landscape composition (proportion of forests, pastures and croplands within 113 ha). To determine the most important habitat-related environmental factors influencing the Sign Encounter Rate (SER) of the three ungulate species, 11 physical, anthropogenic and vegetation variables were simultaneously analyzed through model selection using Akaike's Information Criterion. We found, that *P. tajacu* and *O. virginianus* mainly used early successional stages, while *M. temama* used all successional stages in similar proportions. The latter species, however, used early vegetation stages only when they were located in landscapes mainly covered by forest (97%). *P. tajacu* and *O. virginianus* also selected landscapes covered essentially by forests, although they required smaller percentages of forest (86%). All ungulate species avoided landscape fragments covered by pastures. For all three species, landscape composition and human activities were the variables that

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best explained SER. We concluded that landscape is the fundamental scale for ungulate management, and that secondary forests are potentially important landscape elements for ungulate conservation.

1. Introduction

Neotropical ungulates play an important role in tropical forest ecosystem processes. Through herbivory, seed dispersal and seed predation, they influence forest structure and composition (Galindo-Leal and Weber, 1998), and maintain trophic interactions with large carnivores (Hernández-SaintMartin et al., 2013). Their extirpation from these ecosystems may cause a gradual yet detrimental loss of plant communities and biodiversity likely influencing also people's livelihoods. Conservation of tropical ungulates is challenging, as their natural habitats are ecosystems undergoing the highest rate of land use change globally, which has led to a worldwide expansion of secondary forests. In the 90s, ca. 40% of the global tropical forest surface area was secondary forests (Brown and Lugo, 1990). More recently, it was estimated that the area covered by secondary ecosystems in several tropical American countries exceeded that of primary forests (Chazdon et al., 2009). The precise rate of primary forest transformation, however, is inaccurate because secondary ecosystems are difficult to discriminate from other plant communities with remote sensing tools, and their surface area is often underestimated. Secondary forests will possibly become one of the most wide-spread ecosystem types worldwide in the future (FAO, 2005; Chazdon et al., 2009; Dent and Wright, 2009). Considering that in many cases secondary forests provide the only available refuge for wildlife populations, their overall functional role in habitat provisioning is not well established (Chazdon et al., 2009). Consequently, understanding the influence of different successional stages of secondary forests and that of landscape matrix structure and composition, on occurrence and abundance patterns of ungulate populations may be of great interest for conservation purposes. Although in tropical ecosystems the increase of secondary forests and drastic landscape changes, such as the conversion of forests to croplands and pastures, is a global phenomenon, understanding the key factors for management of tropical ungulates requires detailed studies at local and landscape scales.

The tropical forests in their northernmost extension of Mexico harbor three native ungulate species: the white-tailed deer (*Odocoileus virginianus*), the Central American red brocket deer (*Mazama temama*), and the collared peccary (*Pecari tajacu*). These ungulates are the most hunted species for subsistence in Mexican rural areas, and the white-tailed deer is one of the most-important game species in Mexico (Galindo-Leal and Weber, 1998). Also, since the 1970s these tropical forests have suffered high rates of conversion to croplands and pastures. At the landscape scale, land use change has generated complex mosaics of patches of different successional stages of tropical forest surrounded by a matrix of croplands, pastures, and abandoned lands. Besides the human use of these ungulate species, the transformation of the once forested landscape into an agricultural matrix affects these wildlife species to an unknown extent. Forest transformation alters the spatial distribution, quantity and quality of resources with respect to animal demand (Banks et al., 2007); therefore changes in resource availability will influence habitat use (Morellet et al., 2011). Understanding how these ungulate species select space in relation to landscape composition in areas that have undergone substantial ecological modification, would allow the prediction of ecological responses of these species to global increase of secondary forests. In temperate ecosystems dominated by croplands and pastures, white-tailed deer populations have increased in abundance (Côté et al., 2004) and collared peccaries seem to have adapted well to transformed habitats (Bellantoni and Krausman, 1993). In tropical and subtropical latitudes, however, ungulate population abundances have either declined or become locally extinct (Weber, 2005; Gallina and Mandujano, 2009). Ecological studies of ungulates in secondary tropical forests are scarce (but see DeWalt et al., 2003 and Parry et al., 2007). The majority of ungulate studies in tropical ecosystems have been conducted in protected areas (Naranjo and Bodmer, 2007; Reyna-Hurtado and Tanner, 2007) or in patches of original vegetation in fragmented landscapes (Hill et al., 1997; Peres, 2001; Tejeda-Cruz et al., 2009). Little is known about the effect of intensive land use change and in particular on the role of secondary forests, their vegetation structure and composition, on the distribution and abundance of ungulate species in the tropics. Secondary forests are an important habitat for large vertebrates in fragmented tropical landscapes, especially for disturbance-tolerant species and those with broad diets such as ungulate browsers, which are highly abundant in secondary forests (Parry et al., 2007). Secondary forest serving as wildlife habitat may vary as a function of forest age, and with respect to animal species (DeWalt et al., 2003). White-tailed deer and collared peccary, both generalist species, may readily adapt to human disturbances, as they occur in managed forests, croplands and even in suburban areas (Leopold, 1987; Sowls, 1997). We hypothesized that these species would preferentially use early and intermediate successional stages of secondary forests in areas with low occurrence of mature forests. Contrastingly, specialist species such as the Central American red brocket deer are less tolerant to human disturbances (Bodmer, 1991); hence they are expected to be more abundant in late successional stages than in early and intermediate stages of secondary forests, because late successional stages are more similar to mature forests. Specialist species might be unable to survive on food resources in secondary forests (Parry et al., 2007). In addition to secondary forests, other potential habitats in the landscape, such as old-growth forests, are important for the maintenance of wildlife populations (DeWalt et al., 2003). We expected landscape composition (i.e. proportion of landscape covered by forests,
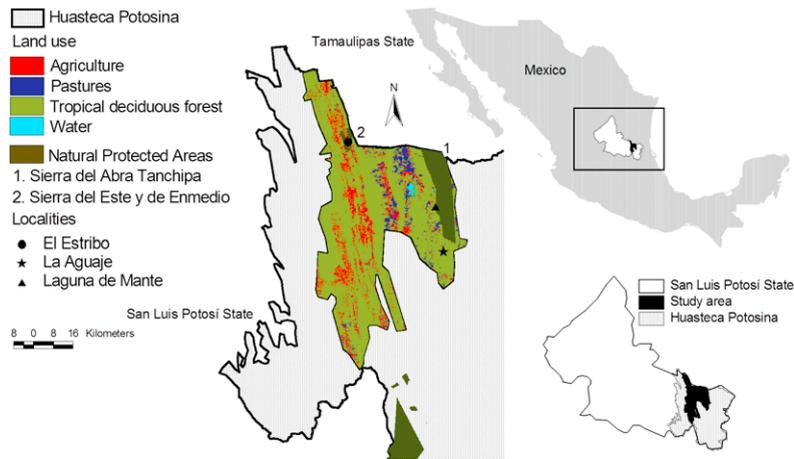
Fig. 1. Location of study area. Land use and land cover, natural protected areas within the region, and localities of ungulate monitoring in the Huasteca Potosina, San Luis Potosi, Mexico.

croplands and pastures, with inherently marked differences in resource quality and quantity) to be another factor influencing habitat use of target ungulates in different ways, depending on their vulnerability to forest disturbance. Central American red brocket deer will select landscapes mainly covered by tropical mature forests (Weber, 2005), while white-tailed deer and collared peccary will select heterogeneous landscapes with small proportions of mature forest. Finally, we expected that the influence of topographic and anthropogenic variables would also influence abundances of target ungulates (see Sanchéz-Rojas et al., 1997, Tejeda-Cruz et al., 2009 and García-Marmolejo et al., 2013). To understand the influence of tropical secondary forest and human activities on ungulates, our goals were three-fold: (1) to evaluate occurrence and abundance patterns in different successional stages of secondary deciduous tropical forest at the local scale; (2) to examine landscape composition (percentage of forest, cropland and pastures) and its effects on the use and selection of these sites by target ungulates at the landscape scale; and (3) to analyze the magnitude of combined effects of successional stages, landscape composition, and topographic and anthropogenic variables on abundance of target ungulates.

2. Methods

2.1. Study area

This study was conducted in three locations in Eastern San Luis Potosi State, Mexico (Fig. 1): El Estribo, Laguna de Mante, and La Aguaje. These sites have low human population densities (<11 inhabitants per km^2) and are located next to two protected areas: Sierra del Este y de Enmedio State Reserve (EER^2; 22°25′N and 99°16′W), and Sierra del Abra Tanchipa Biosphere Reserve (22°15′N and 98°55′W), which include some of the northernmost tropical forests in the American Continent. Climate is warm sub-humid A(w) with mainly summer rains (total annual precipitation: 1009 mm for Sierra del Abra Tanchipa Biosphere Reserve and 1306 mm for Sierra del Este y de Enmedio State Reserve http://smn.cna.gob.mx/emas/) and an average monthly temperature of 24.5 °C. Tropical deciduous forest is the dominant natural vegetation (47% of the region). In many areas, tropical deciduous forests have been replaced by secondary vegetation (Rzedowski, 2006). Early successional stages of these secondary forests are dominated by *Sabal mexicana*, *Guazuma ulmifolia* and *Croton niveus*. In intermediate successional stages, the previously mentioned species are present and dominate the forest canopy together with *Capparis baducca*, *Ardisia escallonioides* and various species of the Fabaceae family. Tree species diversity, tree height and tree trunk diameter increase with increasing age of successional stages such that in later successional stages species of early and intermediate successional stages are replaced by species characteristic of tropical deciduous forests including *Lysiloma microphyllum*, *Beaucarnea inermis*, *G. ulmifolia*, *Phoebe tampicencis*, *Bursera simaruba*, *Myrcianthes fragrans*, and *Zuelania guidonia* (Rzedowski, 2006). A high proportion of the region has been converted to cattle pastures and cropland (mostly sugarcane), which together constitute the matrix surrounding the fragments of tropical deciduous forest. Most tropical ecosystems of this region show some degree of degradation and/or recovery in form of succession (Rzedowski, 2006).

2.2. Sampling units

Within each study location, a gradient of successional stages of secondary forest was selected based on approximate forest age: <14 years (early), >14–<25 years (intermediate), and >25 years (late). Information on forest age was obtained from semi-structured interviews applied to local inhabitants, and based on our observations of plant species composition in each sampling site; the information obtained from the semi-structured interviews was corroborated. A total of 39 permanent

and temporary transects were established for the entire study area. Permanent transects ($n = 27$) each had a length of 500 m, and a width of two meters. The same number of permanent transects ($n = 9$) was assigned to each successional stage, and all three sites had the same number of transects ($n = 3$). Following Mandujano and Gallina (1995), the minimum distance between transects was 500 m. Temporary transects ($n = 12$) did not overlap permanent transects and had a length of 2.5–5 km and a width of two meters. Temporary transects crossed several land use types and successional stages of secondary forests. This approach allowed the comparison of animal tracks among temporary and permanent transects and enabled us assessing whether there were biases in estimates of relative abundance towards areas of secondary forest. Counts of animal tracks were used as an alternative to direct counts of animals with the purpose to monitor species abundance, which is otherwise difficult to determine by direct observation or capture (Nichols and Conroy, 1996).

2.3. Data collection

To obtain ungulate sign records, a total of 85 km were walked. Monitoring was stratified according to successional stage (early, intermediate and late) and seasonal variation including two wet seasons (July–September 2010 and 2011) and two dry seasons (March–May 2011 and 2012). Along each transect, all tracks of the three ungulate species were identified and recorded either individually for the cervids, or as groups for peccaries. Collared peccaries are gregarious, thus, most of the time it was impossible to assign tracks to individual organisms.

At the local scale, variables related to vegetation structure and composition, were measured within each of the three successional stages surveyed. These variables could potentially influence presence and relative abundance of target ungulates. For this purpose, a total of 135 square plots (10 m per side) were sampled. These plots were established along the permanent transects (five per transect). In each plot, all trees with diameter at breast height >5 cm were recorded. For each tree, height was calculated by goniometry (height was estimated as the distance from the tree to a location, where the tree top was sighted from a 45° angle, using a clinometer, plus 1.5 m). Leaf, flower and/or fruit samples from all tree species were collected for subsequent species identification in the herbarium "Isidro Palacios" of the Drylands Research Institute of the Autonomous University of San Luis Potosí, Mexico. Species richness, diversity and stem biomass in each plot were estimated. Biomass was assessed as basal area by tree height by a correction factor (Kramer and Akça, 1995). In the understory, visibility was determined, as a measure of leaf cover for potential protection and resting area. In each plot, a two-meter high cover pole with decimeters marked in white and yellow was placed 10 m distant from the observer. The observed number of counts of bicolor bars on the cover pole was recorded and expressed as percentage of cover (Griffith and Youtie, 1988). Additionally, altitude, using a GPS, and slope, employing a clinometer, were recorded in each vegetation plot.

At the landscape scale, information of relevant environmental and anthropogenic variables was generated from digital cartography. These variables were obtained for each permanent transect, and included distance to nearest human settlement, distance to nearest water source, human population density and density of human settlements within a radius of 3.6 km, and landscape composition (proportion of cropland, pasture, and forest within 113 ha; see Section 3.3).

3. Data analysis

3.1. Characteristics of vegetation structure of successional stages

The eight response variables collected in the plots (see above Section 3.2) were used to determine differences in vegetation structure and composition among the three successional stages. In case the residuals of error terms of the response variables were not normally distributed, transformations were applied. A square root transformation of y plus square root of $y + 1$ was used to normalize the variables slope, tree abundance and tree height, and a fourth root transformation of y was employed to normalize tree species richness and tree diversity (Anderson et al., 2008). For the variables tree density, tree height, and slope, one-way analyses of variance with *post-hoc* Tukey tests were used for mean comparisons among successional stages. Biomass, visibility, and altitude were analyzed using permutation tests for linear models (also called randomization or re-randomization tests). This test is useful when data are sampled from unknown distributions, when sample size is small, and when outliers are present (http://cran.r-project.org/web/packages/lmPerm/lmPerm.pdf). This analysis seemed appropriate for our data, because these variables could not be normalized by transformations. Plant species richness and the Shannon–Wiener diversity index were compared among successional stages for all plots using permutational multivariate analyses of variance (PERMANOVA; Anderson et al., 2008) based on 9999 permutations. PERMANOVA tests allow estimating multivariate variation in a design similar to an analysis of variance through a Pseudo-F statistic using permutations. This analysis is unrestricted by assumptions of normality of error terms and equality of variances and is appropriate for multiple comparisons of community attributes (Anderson, 2001). Differences among individual stages were evaluated with *a posteriori* pairwise comparisons with Pseudo t-statistics. PERMANOVA analyses were performed using PRIMER V6 (Clarke and Gorley, 2006).

3.2. Relative ungulate abundances among successional stages

Relative abundances of each target species were compared among successional stages using only track records found in permanent transects. Generalized linear models with Poisson distribution of error terms were used to compare relative

abundances of each ungulate species among successional stages. This analysis is appropriate for count data whose error terms are not normally distributed (Crawley, 2005). Because the data for the white-tailed deer and the collared peccary showed evidence of overdispersion, the model was re-fitted with *quasi* Poisson distribution of error terms to compensate for the unexplained variation in the response variable (Crawley, 2005). To compare mean ungulate abundances among individual successional stages, multiple comparisons using Tukey's contrasts were conducted. All statistical analyses were conducted in R v. 2.12 (http://www.r.project.org).

3.3. Habitat use by ungulates at landscape scale

At the landscape scale, habitat use was evaluated in units of ca. 113 ha named "landscape units" for this study. This landscape unit size may potentially include at least one home range for the target ungulate species according to home range size estimates by Sanchéz-Rojas et al. (1997), Judas and Henry (1999) and Maffei and Taber (2003). For each species, potential landscape units of 600 m of radius centered around locations of recorded signs along temporary and permanent transects were generated. For the landscape scale assessment, we used all information (including tracks, pellets and sightings) gained on the presence of target ungulates, because considering only tracks associated with different successional stages are irrelevant at this scale. Within each of these landscape units, landscape composition, i.e. the proportion of each of three main land use types in the region, forest, cropland and pasture was calculated using ArcView 3.2 (ESRI, 2002). To avoid possible pseudoreplication arising from landscape units, only records whose buffer areas were only slightly (<20 ha) overlapping were included in the analysis. For this analysis, a total of 32, 64, and 121 presence records were used for the Central American red brocket deer, collared peccary, and white-tailed deer, respectively. This sample of used locations is considered to be a subset of random landscape locations drawn from a larger pool of resource units that were available (Boyce, 2006). To compare landscape units actually used by different ungulate species with potentially available landscape units within the study area, random points within the entire study area were generated. This allowed us estimating if landscape units were being selected relative to what was available (Boyce, 2006) in the region. For this comparison, the same number of random and presence record points for each species were generated, and within 113 ha of each of these points, landscape composition, i.e. the proportion of main land use types, was quantified as described above. The program PREFER 5.1 (http://www.npwrc.usgs.gov) was used to determine the preference of j individuals for i components (i.e. land use types), using availability and usage data as described by Johnson (1980). PREFER tests the hypothesis that all components are equally preferred and compares components using a multiple comparison procedure.

3.4. Effects of habitat-related variables on Sign Encounter Rates

Akaike's information criterion corrected for small sample sizes (AICc), and Akaike weights (W_i; Burnham and Anderson, 2002) were used to evaluate habitat-related effects on Sign Encounter Rates (SER) in permanent transects. SER is an abundance index derived from counts of sign (Nichols and Conroy, 1996) and it was estimated as the number of tracks recorded along each transect divided by its length (n/km). It is assumed that ungulate track impression and disappearance in soil were similar among the species and successional stages. For each target species different combinations of factors and their potential effects on SER were proposed as sets of five, five, and six models, corresponding to respective *a priori* hypotheses, for white-tailed deer, collared peccary, and the Central American red brocket deer, respectively (Table 1). These hypotheses were constructed using environmental and anthropogenic factors as explanatory variables, which affect the distribution of these species at macro-scale in the study region based on previous analyses (García-Marmolejo et al., 2013). The following 11 factors were included in the models: stem biomass, successional stage, visibility, distance to water sources, proportion of forest within 113 ha of tracks, human population size, altitude, slope, tree species abundance, Shannon–Wiener tree species diversity index, and tree species richness. The number of factors for each species was kept at a minimum to avoid model over-parameterization (Burnham and Anderson, 2002). For the Central American red brocket deer, the set of *a priori* hypotheses stated that SER is influenced by: (1) landscape composition, (2) vegetation structure, and topographic characteristics, (3) altitude, and (4) slope. For white-tailed deer and collared peccary, the set of *a priori* hypotheses stated that SER is influenced by: (1) anthropogenic effects, (2) vegetation structure, and (3) landscape composition and successional stage. A global model including all factors from the individual sets of species models was also constructed and used to assess model fit (Burnham and Anderson, 2002). For each species, a null model with only an intercept (*i.e.*, without factors) was constructed. Null models were estimated iteratively with the method of maximum likelihood and were used to determine if inclusion of any of the remaining models would receive more support from the data than a random model.

Akaike differences (∆AICc), and Akaike weights (w_i) were used to rank models from most to least supported by the data. ∆AICc is the difference in AICc between the model with the smallest AICc value and the AICc of each model, and w_i is a measure of support for each model based on ∆AICc that adds to 1 considering all models (Burnham and Anderson, 2002). These values provide direct interpretation of the relative likelihood of a model given the data and the set of candidate models. Then, to account for model-selection uncertainty, model-averaged weighted parameters and their associated standard errors were estimated using w_i as weights as suggested by Burnham and Anderson (2002). Because some variables were more represented in the set of candidate models than others, w_i values were re-scaled according to Burnham and Anderson (2002) to avoid possible model redundancy.

Table 1

Model selection based on Akaike's Information Criterion for the evaluation of effects of environmental variables at multiple scales on SER of three ungulates: *Odocoileus virginianus, Pecari tajacu,* and *Mazama temama* in deciduous tropical forests at the Huasteca Potosina, Mexico during June 2010–May 2012. Number of estimated parameters (K), AICc, weights (w_i), and variables for each model are presented.

Species	Model[a]	K	AIC_c	ΔAIC_c	w_i	Variables included[b]
Mazama temama	LAND	3	16.20	0.00	0.34	fo
	ALTI	3	16.90	0.70	0.24	al
	NULL	2	17.30	1.10	0.20	nv
	SLOP	3	18.60	2.40	0.10	sl
	GLOB	7	19.40	3.20	0.07	bs, ri, al, fo, sl
	VEST	4	20.10	3.90	0.05	bs, ri
O. virginianus	ANTR	5	408.63	0.00	0.51	dw, hp
	LOLA	5	408.81	0.18	0.47	ss, fo
	VEST	6	416.80	8.17	0.01	bs, ab, ri, vi
	NULL	2	418.04	9.41	0.01	nv
	GLOB	11	420.05	11.42	0.00	bs, ab, ri, vi, dw, fo, ss
Pecari tajacu	ANTR	4	156.60	0.00	0.54	dw, hp
	NULL	2	157.40	0.80	0.36	nv
	LOLA	5	159.70	3.20	0.07	ss, fo
	VEST	7	163.10	6.50	0.01	ss, ri, vi, de
	GLOB	10	163.50	6.90	0.01	ss, fo, ri, vi, de, dw, hp

[a] Models: NULL. Null, VEST. Vegetation structure effects, ANTR. Anthropogenic effects, LOLA. Local and landscape scales effects, GLOB. Global model, SUST. Successional stages effects, ALTI. Altitude effects, LAND. Landscape composition effects, SLOP. Slope.

[b] Variables: al. Altitude, bs. Biomass in stems, de. Abundance of trees, dw. Distance to water source, fo. Proportion of forest within a ∼113 ha landscape unit, hp. Human population within ∼40 km², nv. No variables, ri. Richness of trees, sl. Slope, ss. Successional stage, vi. Visibility.

Table 2

Comparison of mean (±standard errors) of elevation and vegetation characteristics among three successional stages in deciduous tropical forests in the Huasteca Potosina, Mexico during the June-2010–May 2012 period. Units of measurement are specified per sampling unit (100 m²).

	Successional stage		
	Early	Intermediate	Late
Abundance of trees (n)	23.2 (±1.19)[a]	36.2 (±0.96)[b]	38.4 (±1.09)[b]
Biomass in stems (m³)	14.4 (±1.58)	17.4 (±1.13)	20.3 (±0.92)
Tree height (m)	5.8 (±0.18)[a]	6.6 (±0.09)[b]	7.8 (±0.18)[c]
Visibility (%)	45.9 (±2.31)	48.7 (±1.52)	45.6 (±1.61)
Richness of trees	7.6 (±0.29)[a]	10.2 (±0.26)[b]	12.1 (±0.33)[c]
Tree diversity index (H′)	1.5 (±0.04)[a]	1.8 (±0.03)[b]	2 (±0.03)[c]
Altitude (m a.s.l)	326 (±4.00)[a]	359.6 (±7.52)[b]	380 (±8.04)[b]
Slope (°)	4.7 (±0.34)[a]	6 (±0.43)	7.1 (±0.45)[c]

a, b, c Different letters between columns indicate significant differences for a given variable.

4. Results

4.1. Differences among successional stages of secondary forests

The three successional stages differed significantly in the following variables: richness of tree species (*Pseudo F* = 4.552, $p \leq 0.0001$, permutations = 9895), tree height ($F = 14.81, p \leq 0.0001$), and Shannon–Wiener tree species diversity index (*Pseudo F* = 4.552, $p \leq 0.0001$, permutations = 9799). These variables increased with age of forest (Table 2). Tree abundance and altitude were both lower in early successional stages in comparison with intermediate and late stages ($F = 22.03, p \leq 0.000$ and $p = 0.0046$, respectively). Slope was significantly smaller in early than late stages ($F = 3.446, p = 0.0348$). Biomass and visibility did not differ among successional stages ($p < 0.05$).

4.2. Ungulate species relative abundances

A total of 867 tracks of the three ungulate species were recorded across all sites. The majority of track encounters were from white-tailed deer. Relative abundances considering successional stages differed significantly only for white-tailed deer with more individuals in early than intermediate stages ($z = -2.307, p = 0.021$), and with more individuals in early than late stages ($z = -1.961, p = 0.0499$). For collared peccary, there were marginally more individuals in early than intermediate stages ($z = -1.933, p = 0.0533$). No significant difference in relative abundance among successional stages was found for Central American red brocket deer. Mean SER in temporary and permanent transects was 6.77 (SE = 1.08) and 3.93 (SE = 0.49) for white-tailed deer, 0.34 (SE = 0.2) and 0.76 (SE = 0.13) for collared peccary, and 0.14 (SE = 0.06) and 0.16 (SE = 0.02) for Central American red brocket deer, respectively. Highest relative abundance was recorded for white-tailed
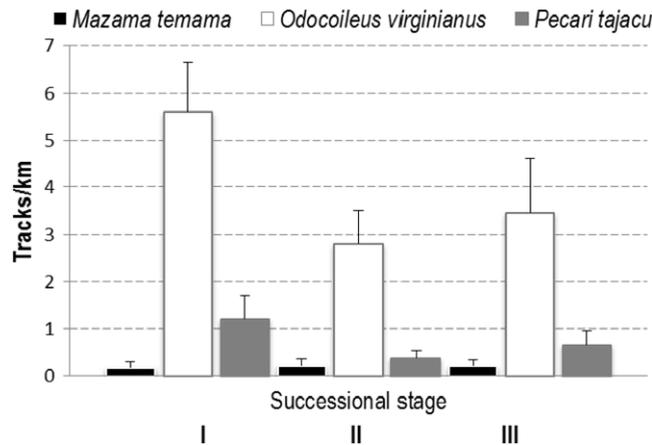
Fig. 2. Relative abundance of ungulates in successional stages. Sign Encounter Rate of *Mazama temama*, *Odocoileus virginianus* and *Pecari tajacu* in three successional stages of the deciduous tropical forest along permanent transects located in the Huasteca Potosina, Mexico between June 2010 and May 2012. Successional stages: I. <14 years (early), II. >14–<25 years (intermediate), and III. >25 years (late). Error bars represent standard errors.

Table 3

Comparison of landscape composition (proportion of forest, croplands, and pasture within ~113 ha) between occupied and available landscape units for evaluating preference by three ungulate species: *Odocoileus virginianus, Pecari tajacu* and *Mazama temama* in deciduous tropical forests in the Huasteca Potosina, Mexico during June 2010–May 2012. The difference in mean rank (variance/covariance) is shown to determine preference between the landscape components, a difference <0 shows a preference for component *i* over component *k*, and >0 a preference for component *k* over component *i*. Absolute standard difference is shown in parentheses.

Components[a] *i/k*	*Odocoileus virginianus*	*Pecari tajacu*	*Mazama temama*
P/A	−0.3886 (1.6865)	−0.4261 (1.5240)	−0.3415 (1.5128)
F/A	−0.1458 (1.2628)	−0.1352 (0.9661)	−0.1442 (0.6009)
F/P	−0.0434 (4.1586)[*]	−0.1047 (3.1568)[*]	−0.1421 (2.4965)[*]
W value	1.85	1.99	2.19

[a] Components: P. Pastures, F. Forest, A. Agriculture.

[*] Statistically significant at $\alpha = 0.05$.

deer (5.6, SE = 1.05) and collared peccary (1.2, SE = 0.28) in the early stage, and for Central American red brocket deer in intermediate and late stages (0.22, SE = 0.14 and 0.22, SE = 0.15). Lowest relative abundances for white-tailed deer (2.8, SE = 0.72) and collared peccary (0.4, SE = 0.13) were recorded in the intermediate stage, and for the Central American red brocket deer (0.18, SE = 0.14) in the early stage (Fig. 2).

4.3. Habitat use related to landscape composition

At landscape scale, significant differences in habitat use were encountered comparing available and occupied landscape units for all three ungulate species ($p < 0.05$; Table 3). These results suggest that all three species show a significant preference for landscapes primarily composed of forest, where pastures constitute a minimal area. Central American red brocket deer showed the highest preference for forested landscapes. On average, this species occupied landscape units composed of 97.9% (SE = 19.4) forest, 1.3% (SE = 0.25) cropland, and 0.7% (SE = 0.14) pastures. Collared peccary and white tailed deer occupied landscape units with 88.5% and 88.4% (SE = 1.18 and 1.01) forest, 6.9% and 6.6% (SE = 0.98 and 0.72) cropland, and 4.6% and 5% (SE = 0.38 and 0.51) pasture, respectively.

4.4. Habitat-related effects on SER at multiple scales

The model that best-supported SER for Central American red brocket deer corresponded to landscape composition effects, however altitude, and the null model received equivalent support as the best-supported model (ΔAICc $<$ 2). For white tailed deer and collared peccary, the best-supported models included anthropogenic effects. Additional models receiving equivalent support as the best-supported model (ΔAICc $<$ 2) included local and landscape effects for white tailed deer, and null effects model for collared peccary. Model-averaged parameter estimates (Table 4) suggested that SER for Central American red brocket deer increased with increasing altitude and with increasing percentage of forest cover in the landscape (Fig. 3(a), (b)). Model-averaged parameter estimates suggested that SER for white-tailed deer slightly increased with decreasing human population density, with decreasing distance to water source, and with decreasing percentage of forest within the landscape. On the other hand, the effect of successional stages on SER was negligible (Fig. 3(c)–(f)). For the collared peccary, model-averaged parameter estimates suggested that SER increased with decreasing distance to water sources, and slightly decreased with increasing human population within 40 km^2 (Fig. 3(g), (h)).

Table 4

Model-averaged parameter estimates and standard errors for three ungulate species: *Odocoileus virginianus, Pecari tajacu,* and *Mazama temama* in deciduous tropical forests at the Huasteca Potosina, Mexico during June 2010–May 2012. Variables used for all models are presented.

Variables	O. virginianus	P. tajacu	M. temama
Intercept	28.497 (±7.66)	7.488 (±4.56)	−0.940 (±1.13)
Biomass in stems	0.614 (±1.54)		−0.018 (±0.05)
Abundance of trees	−1.259 (±3.74)	−2.529 (±1.50)	
Human population	−0.004 (±0.00)	−0.000 (±0.00)	
Intermediate stage	−1.593 (±2.00)	−7.052 (±8.04)	
Late stage	−1.525 (±1.97)	−8.938 (±8.94)	
Richness of trees	−11.858(±14.68)	4.966 (±4.78)	−0.278 (±0.29)
Visibility	3.963 (±6.14)	−1.850 (±2.22)	
Water sources	−0.001 (±0.00)	−0.002 (±0.00)	
Proportion of forest	−0.217 (±0.08)	−0.431 (±0.46)	0.041 (±0.03)
Altitude			0.005 (±0.00)
Slope			−0.103 (±0.11)

5. Discussion

### 5.1. Relative ungulate abundance in tropical ecosystems

We found overall rather low relative abundance of Central American red brocket deer in the Huasteca Potosina and we are not certain, if this is due to massive ecological transformation processes occurring in this region. Our results suggest that this species occupies mostly forested landscapes as reported by Weber (2005), evidencing its vulnerability to deforestation processes occurring in the region and elsewhere in the tropics. White-tailed deer had the highest relative abundance in the Huasteca, in comparison with the other ungulate species. Tropical forests are sub-optimal habitat for the highly adaptable white-tailed deer, while secondary tropical forests contain suitable habitat for this species, and this is the main reason for its expansion into tropical ecosystems (Leopold, 1987). Populations of white-tailed deer benefit from habitat transformation in tropical forests of southern Mexico (Naranjo and Bodmer, 2007). In the Huasteca Potosina, land use change dynamics may have partially contributed to the observed patterns of relative abundance of this species in our study. At present, approximately 35% of land in the Huasteca Potosina is dedicated to agriculture and livestock production. Our data suggest that habitat transformation is the most important driver promoting abundant white-tailed deer populations. The relative abundance of collared peccary in the Huasteca was higher than that reported for tropical evergreen forests. Usually, this species reaches its highest abundance in tropical deciduous forests, which is the closest to its optimal habitat (Leopold, 1987).

5.2. Habitat use at two spatial scales: successional stages vs. landscape units

Central American red brocket deer used all successional stages of secondary forest, but only if the following two conditions were fulfilled: (1) where we recorded individual trees of *S. mexicana*, a palm tree whose fruits are consumed by this species (*personal observation*). Palms have been considered a keystone species for ungulates in South America (Keuroghlian and Eaton, 2008), (2) where successional stages were surrounded by landscapes almost exclusively covered by forest with low human disturbance. The successional stages at the local scale seemed to be a less important determinant of abundance than landscape composition at a larger spatial scale. Di Bitetti et al. (2008) also discussed the importance of landscape context for *Mazama americana*. They found that for hunting effects, the literature was not consistent, but most studies reporting an effect on this species were conducted in fragmented landscapes (Di Bitetti et al., 2008). Assessments of large-scale effects on this and other ungulates may help understanding species responses to human modified landscapes (Morellet et al., 2011). The preferential use of highly forested landscapes is consistent with the low tolerance of this species to anthropogenic disturbances (Reyna-Hurtado and Tanner, 2007, Tejeda-Cruz et al., 2009 and Weber, 2005).

White-tailed deer selected early successional stages at the local level. It is clear, however, that extensive forest cover at larger scales is needed to maintain suitable habitat for this particular species (see Section 5.3). This species uses clearings, where more food resources are available (Galindo-Leal and Weber, 1998; Fulbright and Ortega, 2006), prefers secondary vegetation even in areas frequently used for hunting, and in general avoids subperennial forest (Reyna-Hurtado and Tanner, 2007). White-tailed deer is a highly plastic species whose diet is extremely variable depending on environmental conditions. In tropical forests, it mainly consumes leaves and stems, and during the rainy season fruit can constitute approximately 40% of its diet (Arceo et al., 2005; Weber, 2005). Secondary forests have higher productivity than primary ecosystems (Brown and Lugo, 1990), consequently, they are used more frequently by this generalist species.

Several authors have concluded that collared peccary is relatively tolerant to both disturbance (Sowls, 1997; Leopold, 1987) and secondary forest mosaics (Peres, 2001; Naughton-Treves et al., 2003). Hernández-SaintMartin et al. (2013) found greater abundance of collared peccary in sites located outside than inside of Sierra del Abra Tanchipa Biosphere Reserve, and in secondary forests distant from settlements. In spite of the apparent lack of differences in use of intermediate and late successional stages by this species, it seems that collared peccary is possibly selecting habitats at a larger spatial scale.
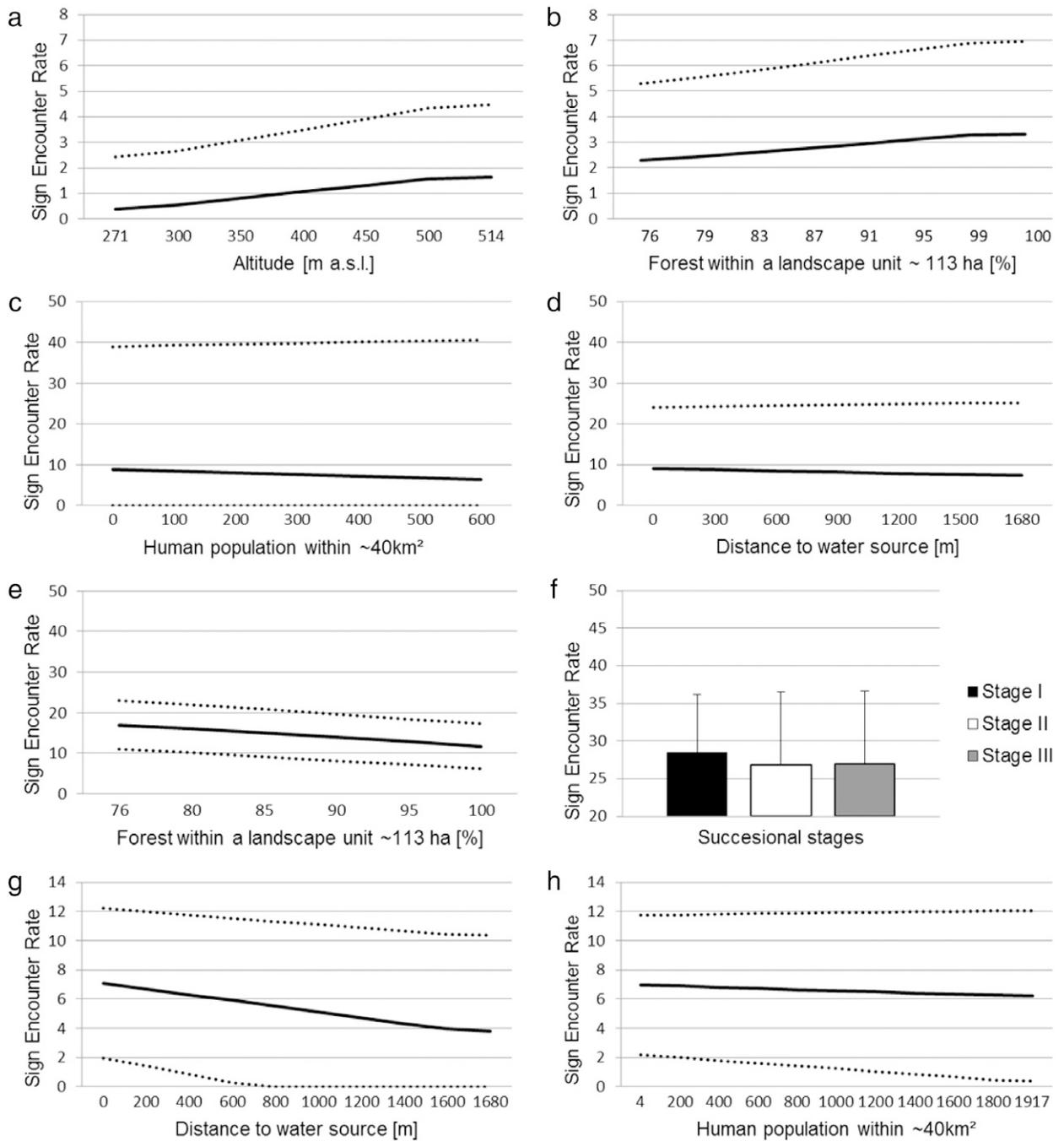
Fig. 3. Habitat-related variables influencing SER for target ungulates. Sign Encounter Rates (number of tracks/km) for *Mazama temama* (a, b), *Odocoileus virginianus* (c*, d, e, f) and *Pecari tajacu* (g, h*) in secondary deciduous tropical forest in the Huasteca Potosina, Mexico during June 2010–May 2012 estimated from model-averaged parameter estimates. Dotted lines indicate standard errors. *Number of inhabitants.

5.3. Habitat-related effects of environmental variables at multiple scales on SER

In the Huasteca Potosina, forests in mountainous terrains with rugged topography are relatively better preserved than those in plains. Hence, the absence of records of Central American red brocket deer near human settlements is not surprising, because remote areas are the most preserved in the study area. These lands, frequently distant from human settlements and with overall low accessibility seem to be an important refuge for this species. Protection status and accessibility have been documented as important variables for the related species *M. americana,* whose abundance increases with increasing distance from access routes, and is higher in areas with protection status (Di Bitetti et al., 2008). These variables may have

a similar effect on Central American red brocket deer. Bolaños and Naranjo (2001) and Weber (2005) reported that in sites with restricted hunting (i.e. those with low accessibility to hunters), the populations of Central American red brocket deer were larger than in hunted sites. All these results are consistent with the current finding that altitude and percent forest cover within a given landscape unit were the most important variables influencing SER.

White-tailed deer and collared peccary selected mostly forested landscapes with only moderate proportions of cropland and pasture. This result supports the hypothesis that both ungulates require forest patches. White-tailed deer uses forests for resting and concealment for rumination and processes related to social interactions such as scent marking (Seagle, 2003), while collared peccary requires habitat with a large proportion of forest and dense understory (Leopold, 1987). In consistency with previous studies (Galindo-Leal and Weber, 1998, Fulbright and Ortega, 2006), our results suggest that this species of deer possesses an opportunistic behavior in terms of usage of cropland and secondary forest, and that it possibly avoids pastures. In tropical ecosystems during dry seasons, a period of low plant growth, 40%–50% of deer diet consists of fruits (Arceo et al., 2005; Weber, 2005). Thus, in these ecosystems diet overlap may be moderate. Livestock impacts on white-tailed deer, however, extend beyond its effect on food, and also include other habitat disturbance effects (Fulbright and Ortega, 2006). Avoidance of pastures is possibly the result of avoiding predation risk by large felids such as the jaguar (*Panthera onca*) and puma (*Puma concolor*) in large open areas, livestock presence, and/or human activity. For collared peccary, it has been documented that this species did not occupy open habitats including pastures, remnant coffee-forests, and remnant pasture-forests (Daily et al., 2003).

Water is an essential habitat component for collared peccary (Sowls, 1997) and for white-tailed deer in arid ecosystems (Fulbright and Ortega, 2006). In the study area, most water sources were artificial. They have been established to supply water for livestock. We documented that in low rainfall years during the dry season, deer frequently visited water ponds. During the rest of the year, plants may suffice to meet their needs (Fulbright and Ortega, 2006). The marginal effect of this variable on SER may be related to intraspecific variation in the use of this resource; however additional studies are needed to examine this hypothesis. In tropical ecosystems, peccaries rarely seem to move far from running water or shallow pools, where they wallow (Sowls, 1997). Water, however, is not an essential resource for this species. Their water requirements are frequently met by their diet; however water reservoirs are important from a behavioral perspective (Carrillo et al., 2002). Wallowing behavior may be a form of grooming (Sowls, 1997), or it may help thermoregulation (Carrillo et al., 2002). In humid tropical ecosystems, collared peccaries wallow in mud. They have permanent and specific wallowing places within their territory (Beck et al., 2010). They create and maintain wallows in lentic bodies of water or depressions in the ground (Beck et al., 2010). Throughout the year, we frequently observed tracks close to water bodies or muddy places, which possibly were used as wallowing spots.

The decrease in SER with increasing human population size has been previously documented for ungulate species. High levels of human disturbance may increase animal movement, and thus changes in foraging behavior. Indeed, human population size has been correlated with hunting, landscape fragmentation, ecological disturbances and intense human activity (Escamilla et al., 2000). Collared peccaries have been reported frequently as being tolerant to human disturbances (Keuroghlian and Eaton, 2008). The current study suggests that although collared peccaries may occupy altered areas, such as early successional stages, they tended to avoid sites affected by intense human activity and were rather recorded in remote areas and also in quite well-conserved areas along temporary transects. It appears that collared peccaries tolerate some human disturbance, but contrary to white-tailed deer, they do not profit from ecosystems altered by anthropogenic activities. Today, despite its widespread geographic distribution and ecological adaptability, populations of collared peccary have significantly diminished and have even been subjected of eradication at local scales due to previous anthropogenic disturbances (Gallina and Mandujano, 2009). Finally, successional stages influenced SER for white tailed deer, but confidence intervals were large. Categorical explanatory variables, such as successional stages, require a larger amount of data to decrease confidence intervals and therefore reduce error.

6. Conclusions

Anthropogenic land use change has apparently altered the natural dynamics of tropical forests in the Huasteca Potosina. The higher than expected relative abundance of white-tailed deer is evidence of a certain imbalance in ecosystem dynamics. In fragmented forests, biodiversity shifts from an original equilibrium to an altered state, mainly as a result of the effects of area reduction and increase in distance to continuous forest or between forested patches (Chiarello, 1999). With time, species diversity will decline and eventually reach a new, less diverse steady state (Lindenmayer et al., 2011). In the altered state, some species such as white-tailed deer may benefit from agriculture and secondary forest. Others, such as the peccary can tolerate moderate levels of human disturbance. Finally, the most vulnerable species such as the Central American red brocket deer may be negatively affected. Specialist species are more likely to disappear than generalists, which in turn may become more abundant. In the future, it will be necessary either to seek system balance through forest restoration, or to maintain an alternative stable state unlikely to shift into an irreversible negative state (Lindenmayer et al., 2011) with unknown effects on human well-being.

Secondary tropical ecosystems offer important resources for ungulate species, however only when these areas are located near forest fragments. Landscape composition appeared to have a greater influence on ungulate abundance patterns and presence/absence than small-scale differences in vegetation structure and composition of secondary forests. Long-term ungulate management should include adequate planning of landscape components and configuration such as forest,

secondary forest, cropland and pastures. The enormous heterogeneity in landscape dynamics and ecological processes are emerging drivers that fundamentally influence resource distribution and selection behavior at different spatiotemporal scales. These are topics for future research.

Effects on SER of ungulates originating from anthropogenic activities such as water reservoirs, human population size, and landscape mosaics related to land use change were more important than the effect of all other biological and physical variables, such as vegetation structure and composition, slope, and altitude. Our results suggest that the future of ungulate populations is closely linked to local decisions for land use change, which are influenced by factors operating at scales related to regional, national and global markets and policies. Wildlife conservation will become effective only if innovative strategies at local scales consider the coupled nature of social-ecological systems. This implies that ecosystems and natural resources management approaches should simultaneously focus on both system components, and on their relationships, interactions, and feedbacks at different spatiotemporal scales allowing incorporating local and more sustainable livelihoods.

Acknowledgments

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