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An Untidy Cover: Invasion of Bracken Fern in the Shifting Cultivation Systems of Southern Yucatán, Mexico

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ABSTRACT

In land change science studies, a cover type is defined by land surface attributes, specifically including the types of vegetation, topography and human structures, which makes it difficult to characterize land cover as discrete classes. One of the challenges in characterizing a land-cover type is to distinguish variability within the class from actual land-cover transformation. The spread of plant invasions in tropical systems is affected by seasonal variations and disturbances such as agricultural activities and fires, making it difficult to determine the spread through thematic classifications. In this paper, we estimate the changes in spatial extent and seasonal variation of bracken fern invasion in Southern Yucatán from 1989 to 2005 by using a linear mixture model (LMM), a widely used method in the classification of remotely sensed data. The results show an increase in areas affected by bracken from 40 km^2 in 1989 to almost 80 km^2 in 2000. Lower estimates of the invasion resulted from data acquired at the end of the dry season (March–May), when bracken mixes with secondary vegetation or is removed by fires. The accuracy of the maps is estimated through the use of sketch maps of farmer's parcels and field data collected from 2000 to 2001. Understanding the spatial distribution and annual variability of bracken fern cover in the region is critical to determining the relation between disturbances such as fire and forest recovery. Using LMM may enhance this understanding by giving a more accurate picture of the extent and distribution of bracken fern invasion.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: fires; invasive plants; land change science; linear mixture model; remote sensing.

INVASIVE PLANTS ARE SIGNIFICANT GLOBAL PHENOMENA that affect biological diversity and ecosystem function (D'Antonio & Vitousek 1992, Mooney & Hobbs 2000, Lugo 2004, Lockwood *et al*. 2007). Invasions occur naturally, but human activity often accelerates invasion rates by several orders of magnitude (Mack 2000, 2005). Land-use studies related to invasive species have usually focused on how land transformation, such as deforestation, drives the spread of such species (Vitousek *et al*. 1997, Hobbs 2000). Recent studies have shown how climate change, combined with disturbances from human activity, will result in feedbacks that further favor the dispersion of invasive species (Vitousek *et al*. 1997, Mooney & Hobbs 2000, Crowl *et al*. 2008). Little attention, however, has been given to the study of plant invasions as an important land-cover change transition (Hobbs 2000), partly because of the difficulty of detecting and monitoring the spatial extent of such invasions (Schneider 2006, Turner *et al*. 2007).

To understand plant invasions, relate them to environmental change, and predict future spread researchers have called for the creation of a global information system that describes not only the ecology and control methods of plant invasions, but also their spatial arrangement (Mack 2000, Richardson & Pyšek 2006, GISP 2008). With an increased interest in the use of earth observations from satellites that provide repetitive and spatially explicit measurements of biophysical surface attributes such as vegetation cover, it seems logical that the spatial arrangement of plant invasions should be determined with the use of such tools (Lambin *et al*. 2006, Bradley & Mustard, 2005, Schneider 2008). Yet, the spread of plant invasions is often hard to characterize into discrete classes. This limitation could result in merging land transformations caused by the spread of invasive plants with more subtle changes that affect a cover without changing the overall characteristics of the landscape (*e.g.*, seasonality). These challenges have motivated the development of continuous land-cover classes, a tool that allows the examination of the trajectory of complex land classes and the detection of the effects of seasonality on vegetation cover (DeFries *et al*. 1999, Roberts *et al*. 2002).

Spatial characterization of plant invasions in tropical landscapes using remotely sensed data is rare. Moreover, land change science studies tend to focus on the thematic characterization of the areas invaded, which has proved to be helpful for monitoring and modeling the invasion (Bradley & Mustard 2005, Huang & Geiger 2008). Mapping plant invasion as a continuous class allows for a better understanding of annual variations of the invasions, which is critical in linking invasions to disturbance events such as fires and land fragmentation. This type of analysis, which has been applied to the study of other land transitions such as deforestation, has shown that changes in land cover are not necessarily progressive and gradual but they exhibit complex trajectories such as periods of rapid and abrupt change followed by a quick recovery (Archard *et al*. 2002, Lambin *et al*. 2006).

Remotely sensed data have proved to be fundamental in characterizing land-cover dynamics due to the spatial and temporal quality of the data sets (Rindfuss *et al*. 2004, DeFries *et al*. 2005). Such data sets strengthen studies in land change science; yet, these tools have been less used by ecologists mainly due to the inability to separate successfully invasive plants from other types of vegetation through spectral signatures (Mack 2005). Also, most of the remote

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sensed data come at resolutions that aggregate landscape attributes, *e.g.*, a 30 m pixel, could contain different types of vegetation and could result in ambiguous characterizations. Some of these issues can be resolved by using linear mixture model (LMM), a technique commonly used in remote sensing when dealing with landscape attributes smaller than the spatial resolution of the sensor. The assumption is that the sensor captures a signal that is the result of a mixture of reflected radiance of the different material found in the landscape, and so the value of the minimum spatial unit (pixel) is the composite spectral signature of surface material such as vegetation, soils, shade and atmospheric effects (Sohn & McCoy 1997, Roberts *et al*. 2002). The interpretation of the data then could be improved by understanding the spectral components within each pixel.

In this paper, we explore the utility of LMM analysis in determining the spatial configuration and variation of bracken fern invasion in the Southern Yucatán. Bracken fern invasion is an important land transition in the region; over the past decade, areas under bracken fern invasion have exceeded the areas under cultivation (Schneider 2006). Frequent fires and land clearance for agriculture have facilitated the replacement of secondary vegetation with bracken fern, while competition between the invasive and native plants through succession has created mixed areas of invasive species and secondary vegetation (Fig. 1). Areas of bracken fern mixed with secondary vegetation have a different spectral response (as detected by satellite sensors) from the areas where either bracken fern or mature vegetation dominates (Roy Chowdhury & Schneider 2004, Schneider 2004). In thematic classifications, however, mixed areas are usually considered either invaded or not, depending on how close the value of reflectance of a pixel is to the mean value for bracken fern cover. This could result in underestimating or overestimating the invasion. Here, we rely on Landsat imagery to examine the utility of using bracken fern and mature forest endmembers to determine the abundance and spatial extent of bracken fern invasion in Southern Yucatán between 1989 and 2005. We explore the interannual variability of bracken fern using data for 1995. Also, for a smaller area in the region, we used multispectral high-resolution data analyzed through supervised classification for 2007 in order to estimate current areas of invasion and relate them to previous patterns. We conclude with a discussion of the ecological implications of the trends of bracken invasion on the region.

METHODS

Study region.—The study region is located at the frontier of the Mexican-Guatemalan border, an area of 3000 km^2, bordering the eastern buffer area of the Calakmul Biosphere Reserve (18°27′ N, 88°50′ W, 100–350 asl). The region is therefore considered a hotspot of tropical deforestation (Lepers *et al*. 2005; Fig. S1). The southern Yucatán region contains the largest tract of continuous deciduous forest in Mexico and it is experiencing an annual rate of deforestation of 0.4 percent, comparable to other forest areas in Central America (Perez-Salicrup 2004, Sader *et al*. 2004). The study region is dominated by two types of seasonal tropical forests: (1) semi-evergreen (semi-deciduous), well-drained upland forests of medium stature with crown heights ranging from 15 to 20 m; and (2) short-statured (5–10 m), less deciduous, seasonally inundated forests (*bajos*) (Martínez & Galindo-Leal 2002, Vester *et al*. 2007). Seasonally inundated savannas characterized by flood-tolerant forbes constitute another land-cover class that dominates to a lesser extent. Other important land-cover classes related to human use are secondary vegetation, mostly fallow, of 4–15 yr; agriculture, which includes pastures, chili and swidden cultivated areas; and bracken fern. Previous research shows that areas invaded by bracken were areas cleared for agriculture and bracken-invaded areas are uncommon in areas surrounded by old growth forest (Schneider 2008).

Currently, land in the southern Yucatán is used mainly for agriculture, followed by pastures and forest extraction. The main activity of farmers is *milpa* cultivation—a polyculture system combining maize, squash and beans. Households are also diversifying their

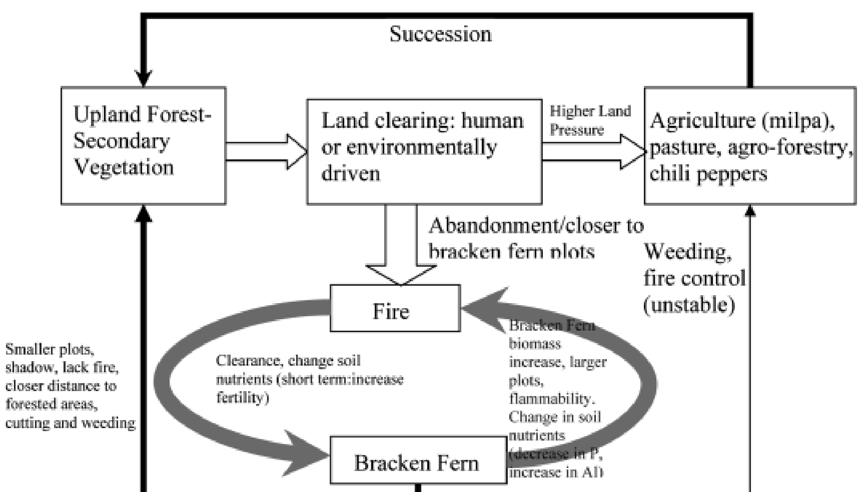

FIGURE 1. Conceptual model of interaction between land-use and bracken fern invasion.

incomes with off-farm activities. After cultivation, or during early stages of fallow, grasses are planted on some land parcels for cattle ranching. Land clearance either for cultivation or for pasture is one of the main drivers of bracken invasion in the region (Schneider 2006).

Bracken fern.—*Pteridium aquilinum* (L.) *Kuhn* has a cosmopolitan distribution (Marrs & Watt 2002). For regions of central and South America a recent revision of the genus reports the presence of *P. aquilinum* var *caudatum* (now *P. caudatum*) (Thomson 2005). Bracken is considered an invasive species because of its tendency to spread out of control, producing a monoculture that discourages the growth of other plant species, thus posing a direct threat to biological diversity. Bracken fern establishes itself on areas dominated by fires, deforestation and agricultural activities, causing severe problems to both farmers and conservationists (Pakeman *et al.* 1996).

The biological adaptability of bracken fern to different environments makes it a successful invader (Pakeman & Marrs 1996, Schneider 2008). Disturbances such as fire and land clearing promote the invasion, and land clearance, fire regimes and land management practices have contributed to the spread of bracken fern in Southern Yucatán (Schneider 2006; Fig. 1). The increase of this invasive could potentially lead to further land abandonment and thus promote greater deforestation (Schneider & Geoghegan 2006). Specifying where bracken fern invades is therefore a critical component of forest conservation and management in the region.

Land clearance has been found to be an important driver of bracken fern invasion, but it is less understood how bracken fern dominates over secondary growth. Possible explanations are that bracken fern invasion competes successfully with secondary vegetation due to frequent fires and, perhaps, soil nutrient limitation (Schneider 2004). Areas of bracken fern that are not continuously burned present a thick ground layer of dry biomass and they can support secondary woody vegetation. However, the added dry biomass makes infrequently burned patches more vulnerable to fires (Fig. 1). These conditions appear to be met in bracken-secondary vegetation parcels at least 3 yr in age. These parcels have enough fuel to support fire ignition and bracken fern spread but are still too young to support secondary trees that can suppress bracken. The analysis of remote sensed data through a linear mixture analysis provides the means to measure the fraction of bracken fern and secondary growth in these invaded areas. Estimating such fractions is critical for determining the possibility of areas invaded to burn and/or recover from invasion.

LMM.—LMM is a common remote sensing technique used to determine the spectral composition of mixed areas (Foody *et al.* 1992, Sohn & McCoy 1997, Roberts *et al.* 2002). The values of reflectance captured within a field of view of the sensor are the result of the reflection of multiple materials that could be decomposed into fractions of several unmixed spectra called end-members (Adams *et al.* 1995). Unmixed spectra or pure cover types when mixed with other covers could be measured by assuming a linear combination of the values of reflectance of the 'pure' constituents in the different spectral bands (Small 2004). Most of the studies that use LMM analysis develop end-members or pure pixels that, combined, will compose the areas of interest, mostly vegetation, nonphotosynthetic vegetation and soils. For this study, we consider invaded bracken fern areas, bright soils and old growth upland forest as end-members. Lowland inundated forest and semi-inundated savannas are excluded from the analysis because these types of forest are not affected by bracken fern invasion; the inundation impedes the growth of bracken fern populations (Schneider 2008). One of the goals of the paper is to explore the utility of the linear mixture techniques when looking at two spectral, separable vegetated covers.

The characterization of bracken fern fractions to determine the spread is based on anniversary dates of Thematic Mapper (TM)-LANDSAT 5 and Enhanced Thematic Mapper-LANDSAT 7 imagery. The imagery was acquired during the period of late November to late January, which corresponds with the beginning of the dry season, few months before fire events are used to prepare land for agriculture. The specific dates are 17 November 1989, 26 November 1995 and 24 January 2000. For 2005, we used data for 19 April, which is the middle of crop establishment. The scene for 2005 is a product developed by USGS—SLC-off gap filling processing which corrects the stripping caused by the malfunction of the sensor after 2003 (Scaramuzza *et al.* 2004). The LMM results for 2005 are affected by the quality of the data set; but they provide a general representation of areas affected by fires and bracken fern. To determine intra-annual variability we analyzed data for 15 March 1995 and compared it with the November image of the same year. All the data are available on the United States Geological Survey's the Glovis visualization viewer (http://glovis.usgs.gov). The individual scenes were originally geo-referenced to a UTM projection (UTM 16, Datum WGS84, Mexico) to under 0.5 pixel RMS error. The scenes were corrected radiometrically by transforming digital numbers to values of reflectance following Chander and Markham (2003). The reflectance bands used in the analysis are those from the visible part of the spectrum (blue, green and red), near infrared (NIR) and two short-wavelength infrared (SWIR-5 and SWIR-7).

End-members were chosen for bracken fern areas, old growth upland forest and bright soils (limestone pits) (Figs. 2 and S2). Pure pixels representing bracken fern, mature upland forest and bright soils were selected from the center of homogeneous plots of these land-cover types. In order to accommodate the dimensionality of the mixing space we include bright soils as an end-member (Small 2004). This implies that bright soils are quite different and unique spectrally from other covers in the region. Between 10 and 15 training sites of 'pure' end-members were defined using on-screen site seeding and compared for consistency. The end-members were located in the same area for all the dates except for areas of soils that correspond to areas where pits for road construction are built. In addition, only few training sites of bright soils were used because they are rare in the region. The training sites used to develop land-cover class end-members come from direct observations in the field obtained in 2000–2001 and 2005 where the locations were recorded using Global Positioning Systems (GPS). Data on land cover for the years before fieldwork were collected through detailed sketch maps of land-use history developed with the help of local farmers (Schneider 2006). All ground truth data were collected

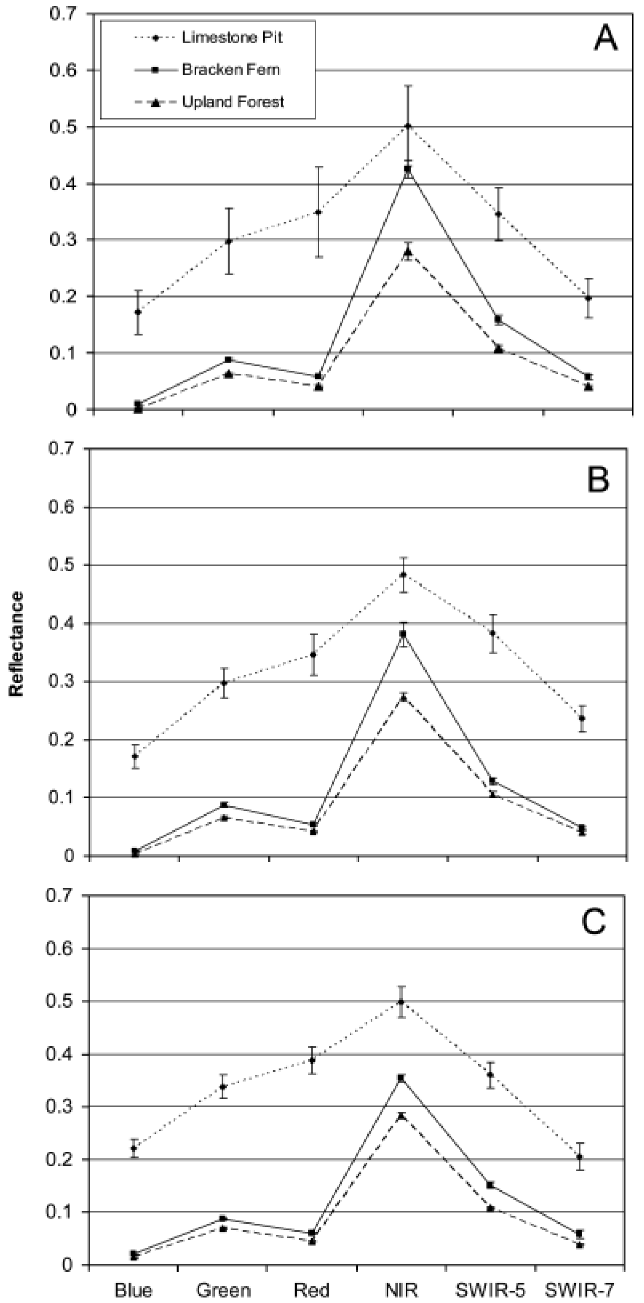

FIGURE 2. End-member spectral signatures from (A) 1989, (B) 1995, and (C) 2000.

through field visits between 2000 and 2001. Topographic and thematic vegetation maps provided additional information on features such as water bodies, inundated savannas and large seasonally inundated *bajos*.

Fractions of the three end-members were estimated using LMM. Specifically, we used the UNMIX command in the GIS software IDRISI-Andes. The program assumes that a pixel value is a combination of the means of the signatures of all the classes present in the pixel—in this case the signatures of the end-members. The calculations are described in Appendix S1. The input for the calculations is the multispectral preprocessed scenes, in our case windowed to the area of interest (36×90 km) and the signatures from end-members. Areas of *bajos*, inundated savannas and water bodies determined by thematic classification were excluded from the area of analysis. The output of UNMIX includes an image for each class defined by the three end-members indicating the percent of that cover in each pixel and a residual image indicating how well the actual pixel values match the calculated mixture of classes (Fig. S3). The higher the residual value, the less likely the calculated mixture is the mixture that actually exists.

The LMM results for 2005 are affected by the quality of the data set, which resulted in misrepresenting the fractions obtained. To determine areas affected by the invasion, we developed a supervised classification for this scene to determine the areas affected by fires that were previously invaded. Then we added the estimation to the final results.

To determine the accuracy of the bracken fern fractions we used field data points collected during fieldwork in 2000 and 2001. For accuracy of 1989 data, we used information from sketch maps developed with the help of farmers. Thirty-one farmers were interviewed and the parcels were geo-referenced with the use of GPS. During each interview, the parcel was walked through and reference points were taken around bracken areas, cultivated plots and boundaries of the parcel. Farmers were asked about the history of bracken fern areas since the first time the parcels were used for agriculture. The locations with bracken presence were used for accuracy assessment. The Kappa Index was calculated for each year based on presence/absence of bracken fern areas in sketch maps. A total of 104 points from the visits were used. From the LMM results, fractions of 50 percent or more were considered to be invaded.

Finally, to evaluate the most recent levels of invasion in the region and to estimate the general trends in the spread we used a multispectral high-resolution quick-bird (3 mts) data set for April 2007. ETM+ cannot be used more recently due to the problem with the stripping errors mentioned before. In the high-resolution data set, the areas affected by bracken are visually and spectrally distinctive from areas of secondary growth and agriculture. The maps developed were also verified by a field visit in January 2008. Areas of bracken were classified using supervised classification. The resulting bracken area mapped from quick-bird was masked and overlaid to the different LMM bracken fern fractions to determine the trend of the invasion (Fig. 3).

RESULTS

Change in cover 1989–2005.—Regional land-cover maps were created to estimate bracken fern fractions from 1989 to 2005 (Fig. S3A). The region overall is experiencing an increase (40 km^2 until 2000) in areas affected by invasion, although a decrease is observed in 2005 (Fig. 3). To tease apart the effect of seasonality and leaf phenology in the final estimations, the LMM analysis is done on data sets that correspond to anniversary dates. The Landsat TM-5 scenes were acquired from late November to late January, which corresponds to the beginning of the dry season and few months after maize cultivation. For 2005 the data used correspond to

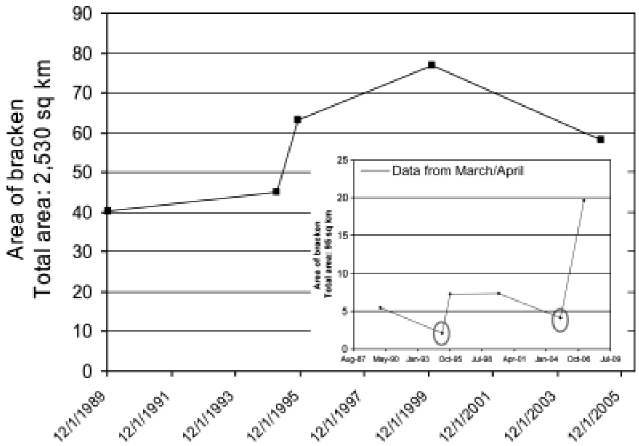

FIGURE 3. Total land affected by bracken fern from 1989 to 2005 from LMM results.

April 2005, at the beginning of land preparation for cultivation, the time when fires are more frequent (J. Rogan et al. unpubl. data). Unfortunately, a high-quality anniversary date scene for 2005 is not available.

In general, the spectral signature of bracken is quite distinct from other types of vegetation in the region (Fig. 2). The signatures for both upland forest and bracken fern follow the same pattern: lower values of reflectance in the red part of the spectrum and high values on the NIR and SWIR. The major difference is observed in higher values of reflectance in NIR for bracken. The value of separability using the transformed divergence index (Richards & Jia 1999) between bracken fern training sites and upland forest was never below 1800. The values of separability range from 0 to 2000 and a value of 1500 or below is considered as a low separability. In general, the larger the magnitude of the transformed divergence index, the greater the statistical distance between training sites and the higher the probability of correct classification (Richards & Jia 1999). Of an average of 12–15 training sites for bracken fern and upland forest used per image, no one has a value of separability < 1800.

The residual maps (Fig. S3B) show that areas with higher values correspond to inundated savannas that were not removed from the initial analysis and areas under cultivation. Higher values indicate that the end-members used in the analysis represent poorly the spectral characteristics of those pixels.

INTRA-ANNUAL VARIATION IN BRACKEN COVER.—A large variation in the amount of area invaded by bracken could be observed between March 1995 and November 1995. The fractions estimated for bracken fern in March 1995 were lower than those in the November scene. For March 1995, some of the invaded areas estimated in November 1995 are burned and areas with higher bracken fractions in November appeared to represent higher fractions of primary vegetation in March. The analysis is only done for 1995 because of the lack of cloud free scenes during the same period for 1989 and 2000.

There is a variation in the fractions and spatial distribution of bracken fern areas within a year. Using a smaller area fitting the quick-bird scene we see a general trend of increase in the total of areas invaded by bracken from 1989 to 2007 (Fig. 3). The fractions, however, are quite different between March and November of 1995. Areas burned in March are not considered to be invaded, but in reality those areas usually get invaded quickly after fires (Fig. S4). Multispectral high-resolution data for 2007 help us illustrate trend and intra-annual variations of bracken fern cover. The data provide a recent point in time which accurately represents spatial distribution of bracken and which we cannot achieve using recent Landsat data sets.

Table 1 shows the values of accuracy of the maps produced for this study. Kappa Index of Agreement (KIA) was calculated for 1989 and 2000. It is usually quite challenging to assess the accuracy of fraction historical land-cover maps due to the lack of ground truth data. Hence, from the historical information gathered through the sketch maps we see that the overall KIA is 0.41. The error of omission, *i.e.*, areas of bracken that were classified as not bracken, is 38 percent, however. For 2000, the error of omission is lower, only 30 percent, and the overall KIA is higher (0.53) than for 1989. The overall KIA for both maps are low compared with other classification analysis. Such low values could be explained in part by the small percentage of total area under bracken—2 percent of total area in the region (Pontius & Schneider 2001). Accuracy results of other LMM studies discuss the difficulty of getting the appropriate ground data and the effect of phenology on the data used for the analysis (Sohn & McCoy 1997, Roberts et al. 2002).

DISCUSSION

Characterizing tropical land covers at a regional level proves to be challenging as land covers in tropical areas are untidy and land transformations are quite dynamic. Unlike hard classifiers such as

TABLE 1. *Kappa Index of Agreement (KIA) for LMM bracken fractions for 1989 and 2000. Numbers in bold are the points where classification and field points are in agreement.*

	Ground truth bracken	Ground truth nonbracken	Total	Error commission
1989				
Bracken fraction	**34**	1	35	0.0285
Nonbracken fraction	21	**48**	69	0.3043
Total	55	49	104	
Error of omission	0.3818	0.0204		
KIA for bracken	0.4079		Overall error: 0.2115	
2000				
Bracken fraction	**49**	9	58	0.1552
Nonbracken fraction	21	**25**	46	0.4565
Total	75	34	**104**	
Error omission	0.30	0.26		
KIA for bracken	0.5254		Overall error: 0.2885	

maximum likelihood that are commonly used to analyze remotely sensed data, soft classifiers such as LMM defer making a unique decision in terms of class membership of any pixel in favor of producing a group of statements about the degree of membership of that pixel in each of the possible classes or end-members (Foody & Cox 1994, Eastman *et al*. 2002). LMM has been commonly used to characterize Landsat 30 m pixels as a combination of very distinct components in the landscape, such as green vegetation, nonphotosynthetic vegetation and bright and dark soils. LMM has proved to be important for local specific studies in discriminating vegetation covers from desert shrubland (Sohn & McCoy 1997) and different types of secondary vegetation in tropical forests of Amazonia (Roberts *et al*. 2002) as well as in determining the abundance of generic attributes, which are not necessarily site specific (Small 2004). Using two types of green vegetation as end-members in LMM, like we do in this study, has not been explored in dense vegetated areas mainly due to the difficulty of finding consistently spectrally pure pixels that have enough difference to be considered end-members.

We attempted to use bracken fern and mature upland forest as two separated end-members because of the presence of large areas of bracken in the region, the spectral separability from other land-cover classes in the region, and the consistency of spectral signature for different years and permanence of patches through time (Fig. S2). The major difference in the spectral response of homogeneous areas of bracken is the higher values of reflectance in the NIR waveband during the beginning of the dry season. Mature upland forest in this region is characterized by high presence of semi-deciduous species. A possible explanation in the difference of values of NIR could be that by the time bracken fern areas are quite established with several layers of individuals and their large leaf extent, they begin to contrast with trees that have smaller leaves and that are beginning to senesce and die at the end of the season. At the end of the dry season, many areas of bracken are burned and bracken fern individuals start to dry up resulting in a spectral response that reflects more areas under agriculture, spectrally showing nonphotosynthetic material and exposed dark soils. To determine bracken fern spread through time the best dates for imagery to be analyzed is during the beginning of the dry season, between November and January.

Research results demonstrate how remotely sensed data analysis is helpful in determining the current extent of bracken fern in the region. Bracken fern displays a unique spectral signature and profile detected by TM and ETM+ sensors. Bracken fern also has a high value of spectral separability from other land-cover classes in the region. Pure stands of the fern larger than a pixel are readily identifiable in the imagery; smaller-sized stands and stands that become mixed with shrubby growth are more difficult to separate from a few other land covers. LMM is useful in determining fractions of bracken within a pixel. Such information is critical to the prediction of future spread and the effects of the spread on fire dynamics in the region (J. Rogan et al. unpubl. data). Areas of bracken fern that are not continuously burned present a thick ground-layer of dry biomass and harbor secondary woody vegetation. The added fuel makes infrequently burned patches more vulnerable to fires. In this case, bracken fern fields exhibit more of a continuum than a well-defined class.

Discrete classes are useful for models predicting the spread of plant invasions as it provides both spatial and tabular measurements to use in common modeling tools (Schneider & Geoghegan 2006). The limitation with discrete classifications arises when the objective of characterizing the spatial patterns is not just predicting but understanding the relations of the invasive with the natural vegetation and land management practices. Understanding these relations is important because it could elucidate the traits that make this invasive so successful in the region.

The results obtained from previous supervised classification analysis (Schneider 2008) show how dense bracken fern areas are distinctive in their spectral signature and relatively easy to identity when well established and frequently burned, because fire removes competitors and creates a homogeneous cover of the fern. Confusion develops where the fern escapes burning for more than 2 yr. In such cases, competitors emerge and complicate the spectral signature of vegetation. LMM analysis is a helpful tool to determine the degree of which bracken fern is mixed with secondary vegetation. Through LMM analysis of a larger time series, we should be able to estimate fire susceptibility of bracken fern fields based on time of establishment.

Based on this study, we think a thematic classification tends to overestimate the area under bracken, forcing some mixed pixels to be considered 100 percent pure bracken. An interesting result to point out is that for March of 1995 a decrease of bracken area is observed, explained mostly by competition with secondary growth. In November of 1995, however, we observe a stepped increase of bracken again. The lower estimate in March 1995 does not imply a decrease in the invasion, but that bracken was suppressed by secondary forest. Fires usually removed such competition from bracken, but due to bracken's vegetative reproductive strategy through rhizomes, areas cleared then were easily and quickly covered again by bracken.

Remote sensing data are helpful to ecologists looking at the spatial patterns of plant invasions. Still there is a need to expand further the study of ecological processes linked to remotely sensed data, which would result in a more accurate understanding of plant invasion and its relation to disturbances. For example, the fractional results of an LMM—ranging from low to high pixel proportions—could be linked to fire frequencies. Preliminary results using fire product from MODIS data show that between 2000 and 2006 areas cover by bracken have the largest fire frequency, followed by early secondary growth areas (J. Rogan et al. unpubl. data). The next step is to determine how mixed invaded areas relate to fire frequencies. If bracken fern areas are more mixed, that could indicate that such areas are more likely to burn than pure bracken areas.

CONCLUSIONS

The general assumption explaining the spread of plant invasions is that land degradation and increases in disturbance promote their spread (Vitousek *et al.* 1997, D'Antonio & Kark 2002). The spatial distribution of plant invasions and the relation with land use, however, may suggest a more complex process. The results in this paper illustrate how remote sensing analysis provides ways to characterize the spatial configuration of plant invasions and to detect important intra-annual variations that relate to the way the invasive relates to the local vegetation.

Most of the research on plant invasions originates in the biological sciences. Those studies focus on understanding the ecological dynamics that promote the invasions, and identify ways of controlling the invasion through land management practices (Higgins *et al.* 1999). Bracken fern has become an important component of the coupled human–environment system of the Southern Yucatán Peninsular Region. Here, secondary vegetation growth is usually rapid with an increase in primary productivity for areas that have been used for agriculture (Read & Lawrence 2003). Even if land uses such as agriculture promote great disturbance, vegetation may still move in and occupy the ground in relatively short periods of time and succession typically proceeds quickly. The ability of the vegetation to reclaim quickly cleared ground allows for the recovery of nutrients in the soil, which enables the success of shifting cultivation, usually involving a long fallow period after a brief interval of cultivation (Turner & Geoghegan 2003). Such process of succession, however, is affected by the ability of bracken fern to dominate after land clearance and fire (Fig. 1).

Previous research considered land use as one of the primary drivers of the increase in plant invasions. Accordingly, socioeconomic factors such as the availability of labor and capital and the dependence of households on subsistence practices determined the willingness or ability of farmers to combat bracken fern invasion (Schneider 2006, 2008). The patterns of plant invasions presented in this paper suggest a more complex relation with disturbances such as fire than being entirely driven by land management decisions. This illustrates how the 'generalities' about land-cover change deriving from a rich array of regional case studies may improve the understanding and modeling of critical themes in global change and sustainability studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Southern Yucatán Peninsular Region. Study Region.

FIGURE S2. (A) Landsat TM-5 composites of Red, NIR and SWIR for 1989 and 2000 showing areas invaded by bracken fern. (B) Close up of areas invaded with bracken fern in eastern Yucatan region from March to November, end of cropping cycle.

FIGURE S3. (A) Bracken Fern Fractions using Linear Mixture Model from 1989 to 2000. (B) Residuals image indicating how well the actual pixel values match the calculated mixture of classes.

FIGURE S4. Changes in bracken fern fractions from March to November in 1995.

APPENDIX S1. Additional methods.

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