Testing Chronosequences through Dynamic Approaches: Time and Site Effects on Tropical Dry Forest Succession

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ABSTRACT

Chronosequences, commonly used to assess succession, have been questioned because of their failure to project successional trajectories. Here, we develop a simple analytical approach combining both chronosequence and dynamic data to test the power of age of abandonment and site factors to explain and predict succession. The approach proceeds by first fitting statistical models relating age to attribute values (the chronosequence model) and their observed changes (the dynamic model) to test explanatory power. Predictive power is then tested by bootstrapping the chronosequence model to derive confidence intervals for expected changes and comparing them with the dynamic model. Finally, residuals from both models are tested against site factors. The procedure was applied to six attributes (basal area, plant density, mean plant height, species richness, evenness, and composition) of the woody community (plants >1 cm dbh within 0.1-ha plots) in nine abandoned cattle pastures (0–12 yr) and three old growth tropical dry forests monitored over 6 yr. Age explained 60–97 percent of the variance in community attributes and only 32–57 percent in observed changes. It significantly overestimated basal area and mean height, while species richness and composition were highly predicted. Besides age, management history also explained successional dynamics. Our results suggest age is not necessarily a reliable predictor of short-term successional dynamics, and explanatory power is not indicative of predictive power. Because of this low reliability, caution is needed when applying chronosequences to evaluate ecosystem services’ recovery. The analytical approach developed here contributes to a better exploration of those possible limitations.

Abstract in Spanish is available in the online version of this article.

Key words: Chamela; land use history; Mexico; nonlinear models; rates of change; soil conditions; successional trajectories; surrounding matrix.

Secondary forests will likely dominate future tropical landscapes. Old growth tropical forests have been transformed mainly for the expansion of agriculture (Geist & Lambin 2002, Sanchez-Azofeifa & Portillo-Quintero 2011), but agricultural fields are often abandoned because of productivity loss or change in socioeconomic context (Wright 2005). Secondary forests developing in these abandoned fields are becoming increasingly representative of tropical landscapes, reclaiming up to one-third of the original deforested area (Wright 2005, Foley et al. 2007). Understanding how these forests change in the course of succession is critical for ensuring biodiversity conservation and maintaining the supply of ecosystem services in tropical regions (Barlow et al. 2007, Chazdon et al. 2009).

Research on secondary succession in abandoned agricultural fields has mostly relied on the use of the chronosequence approach, where successional change is inferred by relating the time since field abandonment to plant community attributes such as basal area, biomass or species richness (Pickett 1989, Walker et al. 2010). The chronosequence approach, however, has been challenged (Johnson & Miyaniishi 2008). First, there is large variation in the explanatory power of age of abandonment, associated with differences in previous use or environmental conditions among sites (Marín-Spiotta et al. 2008, Mwampamba & Schwartz 2011, Dupuy et al. 2012), or with the community attribute being analyzed (Chazdon 2008, Lebrija-Trejos et al. 2008, Muñiz-Castro et al. 2011). Second, there is an apparent inability to project successional trajectories, since changes over time in ecosystem attributes do not necessarily match successional trajectories or rates of change inferred from chronosequences (van Breugel et al. 2006, Chazdon et al. 2007, Feldpausch et al. 2007, Maza-Villalobos et al. 2011, but see Foster & Tilman 2000). These challenges raise questions about the particular situations and variables for which chronosequences would adequately describe successional change (Walker et al. 2010) and, therefore, about its applicability to project the recovery of ecosystem attributes such as biomass and carbon stocks (Feldpausch et al. 2007, Johnson & Miyaniishi 2008).

An improved understanding of succession could be achieved if chronosequences were complemented with a dynamic approach by monitoring sites through time. This would allow for a test of the match between successional trajectories projected from chro-
nsequences and those derived from repeated measurements (Pickett 1989, Foster & Tilman 2000, Chazdon et al. 2007). However, there are relatively few dynamic studies of tropical succession (Chazdon et al. 2007, Lebrija-Trejos et al. 2010, Williamson et al. 2012). In addition, there is a lack of adequate, statistically based tests for chronosequence-based inferences (Feldpausch et al. 2007, Johnson & Miyanishi 2008). Tests have mostly relied on the visual comparison of the trajectories from chronosequence and dynamic observations or on correlations between age of abandonment and observed community changes (Foster & Tilman 2000, Chazdon et al. 2007, Maza-Villalobos et al. 2011, Williamson et al. 2012). These approaches do not test for specific trajectories or rates of change expected from chronosequence models.

The effect of site factors should also be taken into account to improve our understanding of succession. There is extensive evidence suggesting that factors like field management history, soil properties, and adjacent forest cover can influence succession (Holl 1999, Guargiuta & Ostertag 2001, Chazdon 2003, 2008). Their effects may depend upon the attribute analyzed. Species diversity and composition are expected to be dependent primarily on both the presence of remnant vegetation, and on the properties of the forest matrix around sites (Purata 1986, Holl 1999, Norden et al. 2009). On the other hand, structural attributes have shown to be highly influenced by previous land use, particularly the type of land clearance or the frequency of fires (Uhl et al. 1988, Moran et al. 2000), although they can also influence species composition (Mesquita et al. 2001). Most of the chronosequence studies, however, rely on the assumption that sites are under similar conditions, and only a few have addressed those site effects, particularly for tropical dry forests (Uhl et al. 1982, 1988, Moran et al. 2000, Powers et al. 2009, Mwammba & Schwartz 2011, Dupuy et al. 2012). Since chronosequence’s failure to project successional dynamics could be explained by subtle differences in site conditions, testing this assumption is relevant in explaining successional patterns and the usefulness of the chronosequence approach.

To advance our understanding of the power of age of abandonment and site conditions to explain and predict changes in forest attributes along succession, we developed a model-based analytical approach combining chronosequence and dynamic data to test chronosequence explanatory power and its predictions of successional dynamics. We then applied this procedure to study secondary succession of tropical dry forest (TDF) woody communities in abandoned cattle ranching pastures of western Mexico. Six different community attributes were analyzed: basal area, plant density, height, species richness, species evenness, and species composition. We further assessed the role of site factors like field management history, soil condition, and adjacent forest cover in explaining successional patterns of these attributes. Specifically, we tested the following: (1) whether age of abandonment is a major explanatory variable of among-site variability in community attributes and their observed net changes; (2) to what extent chronosequence models predict net changes in community attributes observed over 6 yr; and (3) to what extent site factors other than age of abandonment explain variability in community attributes and their observed changes over time.

METHODS

ANALYTICAL APPROACH.—The main hypothesis behind the chronosequence approach is that time since field abandonment constitutes a major explanatory variable for differences in community attributes across sites. Testing this hypothesis commonly proceeds through fitting a statistical model relating the observed chronosequence data to age of abandonment (i.e., a chronosequence model). If chronosequence assumptions were met (sites are under the same biophysical conditions and subjected to similar management regime), we would expect site dynamics to parallel the trajectory or present a trend similar to that predicted by the chronosequence model. Consequently, a test of the predictive power of a chronosequence could proceed by calculating observed community changes from repeated measurements over a given time period and comparing them with expected changes derived from the chronosequence model. Here, we develop and apply an analytical approach following this rationale.

The analytical approach can be summarized in seven steps. In step 1, a chronosequence model is fitted to explore if age of abandonment explains variability in attribute values among sites. In step 2, a confidence interval for the chronosequence model is calculated from a family of fitted models generated by bootstrapping samples. Step 3, expected net changes in attribute (NCexp) are calculated from the chronosequence model as NCexp = A\text{f} + ΔA where A\text{f} is the attribute value calculated from the model at a given age (time = t), and ΔA is the value of such a trait at Δt yr. Step 4, confidence intervals for the NCexp are obtained by applying step 3 to the family of models from bootstrapped samples obtained in Step 2. Step 5, observed net changes in attribute (NCobs) for each site are calculated as the difference between two repeated measurements separated by the Δt period. A ‘net change model’ relating NCobs to age at first measurement is then fitted to explore to what extent age explains variability in observed net changes among sites. Step 6, test of the predictive power of the chronosequence on the observed successional dynamics is done by comparing the mean and confidence intervals for NCexp (steps 3 and 4) with the net change model (step 5). Step 7, linear models are used to relate residuals from the chronosequence and net change models to site variables to assess the importance of site factors on succession beyond age effects. Further details on the analytical approach and an R code for its implementation are provided in Appendix S1.

TEST OF THE CHRONOSEQUENCE USING TROPICAL DRY FOREST DATA.—We applied the analytical approach to a case study of TDF secondary succession conducted in the Chamele-Cuizamla Biosphere Reserve (CCBR) and adjacent areas, on the Pacific coast of the state of Jalisco, Mexico (19°23′–19°30′N, 104°56′–105°04′W). Mean annual temperature is 24.6°C, and mean annual precipitation is 788 mm, with a severe drought season from November to May (García-Oliva et al. 2002). Because of rainfall
seasonality, most of the landscape is covered by TDF from 5 to 10 m high (Sanchez-Azofeifa et al. 2009). Areas adjacent to the CCBR have been transformed mainly into pastures for cattle raising during the past 40 yr (Maass et al. 2005). Those areas are often left without maintenance, resulting in the development of secondary forests (Burgos & Maass 2004).

A chronosequence was established with nine secondary forests from abandoned pastures and three old growth forests sites (without evidence of recent human disturbance). Sites were located at northwest and southeast extremes of the CCBR in order to include possible regional variations in climate or soils associated with geologic origin or topography (García-Oliva et al. 2002, Schaaf 2002). All of the sites were located on slopes (15° to 30°) to represent the dominant topographic condition (Balvanera et al. 2002, Cotler et al. 2002) and faced south (southeast to southwest) to represent the most extreme conditions in terms of high evaporative demand (Balvanera et al. 2002). All secondary forests were located in sites where land was used mainly for cattle ranching (from 4 to 28 yr after slash and burn of the former old growth forest) with repeated burning, planting of exotic grasses and free grazing. Age of abandonment varied between 0 and 12 yr by November 2004 (assessed through interviews with owners), when permanent plots were established and sites fenced with barbed wire to exclude cattle.

At each site a 20 m × 50 m plot was established. All woody plants including trees, shrubs and lianas, and arborescent cacti (henceforth all will be referred to as woody community) were tagged, identified and measured for diameter at breast height (dbh) in 2004 (we measured the diameter at the base for lianas, which will be hereafter referred to for all as dbh). Plant height was measured since 2007 (excepting lianas). A size-stratified sampling was used: stems with dbh ≥1 cm were sampled in half of the plot (10 m × 50 m) and those ≥2.5 cm dbh in the other half. Two additional censuses were carried out in 2007 and 2010 following the same sampling protocol.

For each plot and census year, we assessed structural attributes, as well as species diversity and species composition. Structural attributes included basal area, plant density and plant mean height (the latter only for plants with at least one stem ≥2.5 cm dbh). Diversity attributes were rarefied species richness (for 50 individuals per plot) and evenness (using Hurlbert’s Probability of Interspecific Encounter), both calculated using EcoSim (Gotelli & Entsminger 2011). Species composition was reduced to a continuous scale by applying a non-metric multidimensional scaling ordination (NMDS) to a Chao-Sorensen matrix of dissimilarities for the data from the three censuses and 12 sites; site scores for the first ordination axis were then employed to represent species composition for each site/year combination. Stress value obtained was 0.021. NMDS was performed using the ‘metaMDS’ function in the vegan package for R (Oksanen et al. 2013).

Chronosequence models in step 1 were fitted using data from 2004. For each attribute, four different nonlinear models were tested: Michaelis-Menten, asymptotic, Gompertz and logistic (Table S1). In all models, old growth sites were included by setting their age as 100 yr, since model parameter estimates did not change by more than 0.1 percent when old growth forest age varied between 50 and 500; other studies have used a similar criterion (Peña-Claros 2003, Becknell et al. 2012). Model fitting was performed using ‘nls’ function in R (R Core Team 2013). The best-fitted model for each community attribute was selected based on the AICc. For the net change models, the form of the model corresponded to the first derivative of the best-fitted chronosequence model (Table S1). Confidence intervals for model parameters were calculated based on 1000 bootstrapped samples for each model. Observed and expected net change (NC) in steps 3–5 were calculated for Δt = 6 for all attributes except mean plant height, in which case Δt = 3 yr.

Residuals from both the chronosequence models and the net change models were related to field management history, soil condition, and adjacent forest cover of the sites (step 6). Management previous to plot establishment, characterized through semi-structured interviews with landowners (Trilleras 2008), was summarized into variables describing the frequency, magnitude, intensity and duration of agricultural, pastoral and extractive activities (Appendix S3). Physical and chemical soil properties as well as soil degradation status were assessed from one soil profile in each site (Appendix S3; Trilleras 2008). Adjacent forest cover (by differentiating forested and non-forested areas) was quantified using true color imagery from 2003, downloaded from Google Earth® and interpreted using Arcmap® for buffers of 100–300 m (Appendix S3); these distances cover the spatial range at which most seed wind dispersal occurs (Contreras-Sánchez et al. 2011).

Site variables were subject to an ordination procedure to reduce their dimensionality and to ensure orthogonality. Ordination was performed using the ‘dudi.mix’ function in the ade4 package for R (Dray & Dufour 2007), which allows for the inclusion of continuous, ordinal and categorical data in the same analysis. Residuals from models were then related to ordination axes using linear models. The first three ordination axes, which explain 57.5 percent of variation in site variables, were tested (Table S2). We used the ‘limp’ function in the ImPerm package for R (Wheeler 2010), which employs permutation tests to obtain P-values for the models without assuming normality. We included only the nine secondary forests in this analysis since management was meaningless for old growth forests. Finally, pairwise associations were tested among residuals from chronosequence models or net change models and those site variables that significantly correlated with the ordination axes. Associations were tested using Spearman correlations when site variables were quantitative or net change models and those site variables that significantly correlated with the ordination axes. Bonferroni corrections were then applied to P values of the pairwise associations in order to avoid this inflated probability.

Test of the chronosequence using a simulated dataset.—We assessed the performance of the analytical approach by applying it to three different simulated repeated measurements’ datasets.
RESULTS

AGE OF ABANDONMENT AS AN EXPLANATORY VARIABLE OF COMMUNITY ATTRIBUTES AND THEIR OBSERVED CHANGES.—Chronosequence models showed that age of abandonment had a high explanatory power for all of the six attributes of the TDFs. Overall, age explained 60–97 percent of the differences in community attributes across sites (Table 1A). Structural attributes, namely basal area, plant density and mean plant height, were better explained by age ($R^2 = 0.79–0.97$) than were species richness, evenness and species composition ($R^2 = 0.60–0.80$; Fig 1; Table 1A). Basal area and plant density showed a sigmoid trajectory (Fig. 1A and B), while the other attributes exhibited a more asymptotic one (Fig. 1C–F).

Observed net changes in community attributes ($NC_{obs}$) were partially explained by age of abandonment (Table 1B). Age explained $NC_{obs}$ better for species richness, evenness and composition ($R^2 = 0.53–0.57$) than for structural attributes ($R^2 = 0.06–0.40$). Net change models for basal area and plant density described a humped pattern in relation to age (Fig 2A and B), while those of other attributes describe a negative trajectory (Fig. 2D–F). The $NC_{obs}$ for mean plant height did not show any relation to age (Fig 2C; Table 1B).

CHRONOSEQUENCE POWER FOR PREDICTING OBSERVED ATTRIBUTE CHANGES.—Net change models for the woody communities in the TDF’s described successional trajectories that fell consistently below the expected trajectories for basal area, plant density, mean height, and species composition (Fig. 2). On the contrary, the $NC_{obs}$ trajectory for evenness was consistently above the expected one. Overestimation was significant for two structural attributes, basal area and mean plant height, as trajectories defined by their net change models fell outside confidence intervals of the $NC_{exp}$ trajectories (Fig. 2A and C). In contrast, chronosequence attribute models adequately predicted those $NC_{obs}$

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Term 1</th>
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<th>Term 3</th>
<th>RSE</th>
<th>$R^2$</th>
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<tbody>
<tr>
<td>Basal area</td>
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<td>4.29**</td>
<td>0.80**</td>
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<tr>
<td>Plant density</td>
<td>Logistic</td>
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<td>5.51**</td>
<td>2.38**</td>
<td>822</td>
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<tr>
<td>Height</td>
<td>Logistic</td>
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<td>-0.75</td>
<td>5.69**</td>
<td>0.616</td>
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<td>Rarefied richness</td>
<td>Logistic</td>
<td>24.87**</td>
<td>1.16</td>
<td>4.44**</td>
<td>2.86</td>
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<tr>
<td>Evenness</td>
<td>Logistic</td>
<td>0.94**</td>
<td>-15.02**</td>
<td>6.89**</td>
<td>0.031</td>
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<tr>
<td>Composition</td>
<td>Logistic</td>
<td>1.39**</td>
<td>4.91**</td>
<td>5.11**</td>
<td>0.279</td>
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</table>

<table>
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<th>Model</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\gamma$</th>
<th>RSE</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area</td>
<td>Gompertz</td>
<td>38.12**</td>
<td>3.56**</td>
<td>0.56**</td>
<td>2.40</td>
<td>0.32</td>
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<tr>
<td>Plant density</td>
<td>Logistic</td>
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<td>2.42</td>
<td>0.79**</td>
<td>1.380</td>
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<td>Height</td>
<td>Logistic</td>
<td>1.06</td>
<td>6.26**</td>
<td>1.09**</td>
<td>0.044</td>
<td>0.06</td>
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<tr>
<td>Rarefied richness</td>
<td>Logistic</td>
<td>95.4**</td>
<td>2.63</td>
<td>3.84**</td>
<td>2.27</td>
<td>0.57</td>
</tr>
<tr>
<td>Evenness (PIE)</td>
<td>Logistic</td>
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<td>-1.13</td>
<td>5.92*</td>
<td>0.002</td>
<td>0.53</td>
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<tr>
<td>Composition</td>
<td>Logistic</td>
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<td>5.56*</td>
<td>2.53**</td>
<td>0.081</td>
<td>0.53</td>
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</table>

Significance levels are **$P < 0.01$ and *$P < 0.05$. 

Models fitted to community attributes were selected on the basis of minimization of AICc from four possibilities: Michaelis-Menten, Asymptotic, Gompertz, and Logistic.

Models fitted to observed net changes correspond to the first derivatives of selected chronosequence models.
trajectories for two species-based attributes: rarefied richness and species composition (Fig. 2D and F). NC obs trajectories for plant density and species evenness fell partially inside the confidence interval (Fig. 2B and E).

SITE FACTORS INFLUENCING SUCCESSION.—Ordination axes derived from site factors did not explain residuals from chronosequence models, but partially explained residuals from some net change models (Table 2). The residuals of the model for net changes in mean height were related to ordination axis-3 (Table 2), which in turn was linked to different aspects of forest clearing, cattle grazing regime, and extraction of timber (Table S2). Residuals of the models for net changes in species richness and composition were related to ordination axis-2 (Table 2), which was related to different aspects of field management, cattle activity, soil condition, and adjacent forest cover (Table S2). For these three net change model residuals, we found significant correlations with site variables associated with ordination axes-2 and 3 (Fig. 3). For mean plant height, residuals increased as years since last slash increased (Fig. 3A). Residuals from species richness decreased as the extension of forest clearing increased or when no herbicide was applied for weed control (Fig. 3B and C). Finally, residuals from species composition decreased as the duration of cattle grazing and timber extraction duration and extension increased (Fig. 3D–F). Adjacent forest cover variables did not show any significant association with residuals, although coverage in 200 and 300 m buffers were associated with axis-3 (Table S2). Adjacent forest cover variables were highly correlated with age of abandonment (Spearman rank correlation coefficients = 0.63 \(P < 0.01\), 0.70 \(P < 0.05\), 0.77 \(P < 0.05\) for buffer areas of 100, 200 and 300 m radius, respectively.

PERFORMANCE OF THE ANALYTICAL APPROACH USING SIMULATED DATASETS.—Both the amount of random or systematic error in site trajectories caused significant and consistent divergence between observed and expected net changes (Figs. S2 and S3). Variation in sample size had less effect on divergence between chronosequence and dynamic approaches, with small sample sizes sometimes leading to partial departure from chronosequence expectations (Fig. S1).

DISCUSSION

AGE OF ABANDONMENT AS EXPLANATORY VARIABLE OF COMMUNITY ATTRIBUTES AND THEIR OBSERVED CHANGES.—Age of abandonment was clearly a major factor explaining variation in community attri-
butes based on chronosequence data in secondary TDFs in Chamela. Similar results have been observed in other chronosequence-based studies where sites were selected with similar criteria, i.e., seemingly homogeneous environmental and historic conditions (Peña-Claros 2003, Lebrija-Trejos et al. 2010, Muñiz-Castro et al. 2011). The explanatory power of age, however, varied with the attribute analyzed: it was higher for structural attributes than for diversity and composition. Structural attributes have been shown to recover independently from the number or identity of species and to be less susceptible to deviation from the expected successional trajectory defined by age (Pascarella et al. 2000, Molina-Colon & Lugo 2006, Martin-Spiotta et al. 2007). Perhaps once a minimum set of species spanning over a range of functional responses is present, the recovery of forest structure proceeds in a more deterministic way, only loosely associated with the number or identity of species (Yachi & Loreau 1999, Lasky et al. 2014). The addition of new species seems necessary, though, to sustain forest recovery over time (Allan et al. 2011).

Age of abandonment also explained variation in dynamic data, i.e., observed attribute net changes across sites, but with lower explanatory power than for community attributes. Differences in explanatory power may be related to the effect of water availability at different time scales. Regarding rates of change, the study of the seedling community in the same chronosequence has shown that they are not related to age but rather to interannual variation in precipitation patterns (Maza-Villalobos et al. 2011, 2013). In the case of community attributes, studies of the conserved forest show that they are clearly correlated with

| TABLE 2. Linear models testing for the effects of site factors on residuals from chronosequence models and net change models shown in Table 1. Only those residuals with significant effects are shown. Site variables assessing management history, soil condition, and adjacent forest cover (see Appendix S3) were reduced to three ordination axes (A1–A3) which were further included in the models. The Coeff i column refers to model parameter relating residuals and age of abandonment. RSE is residual standard error, R^2 is coefficient of determination and NCobs are observed net changes. Significance codes: ** P < 0.01 and * P < 0.05 |
|----------------|----------------|----------------|----------------------|
| Model residuals | Axis | Coeff i | RSE | R^2 |
|----------------|----------------|----------------|----------------------|
| Height NCobs | A-3 | 0.039* | 0.051 | 0.44 |
| Richness NCobs | A-2 | 0.277* | 0.273 | 0.58 |
| Composition NCobs | A-2 | 0.009* | 0.010 | 0.51 |

FIGURE 2. Net changes (NC) in community attributes as a function of age of abandonment of secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. Dots represent observed net changes for each site, calculated for the 2004 through 2010 period (2007–2010 for plant mean height). Gray continuous lines represent the net change models fitted to observed changes. Black continuous lines represent expected attribute changes from chronosequence models fitted to community attributes (see Fig. 1), with dotted lines being their 95% CI limits. OGF refers to old growth forest sites.
topographically driven differences in water availability (Lott et al. 1987, Segura et al. 2003). It then seems that while net changes in attributes may respond to short-term (interannual) water availability, which is highly variable and not related to age, community attributes could be representing the effect of historical average water availability captured by age of abandonment.

**MATCH BETWEEN OBSERVED AND PREDICTED CHANGES IN COMMUNITY ATTRIBUTES THROUGH TIME.**—Our results suggest that chronosequence models have less power to predict short-term successional dynamics for forest structural attributes than for species identity-based attributes like diversity or composition. The two attributes significantly and consistently overestimated by chronosequence models, namely basal area and mean plant height, are structural attributes. The third structural attribute (plant density) was also overestimated along all the age range evaluated, although not significantly. On the contrary, species-based attributes were not significantly over- or underestimated, although species evenness and composition net change models fell partially outside intervals predicted from chronosequences.

These results contrast with the explanatory power of the chronosequence models, for which structural attributes like basal area and plant density had higher $R^2$ values, but did not perform better in predicting observed net changes than species-based models like evenness and composition with lower $R^2$. Therefore, there seems to be no relation between $R^2$ values of the chronosequences and their predictive power. These findings contradict the generalized view that chronosequence models predict changes of structural attributes, particularly basal area, better than those of diversity or taxonomic composition (Chazdon et al. 2007, Quezada et al. 2009). This view is mostly based on the commonly high $R^2$ values found for structural variables when using chronosequence approaches. Other studies, however, have also shown wide variation in the predictive power of the chronosequences with strong departures of the observed from the expected trajectories (Breugel et al. 2006, Chazdon et al. 2007, Feldpausch et al. 2007) as well as close matches (Foster & Tilman 2000, Lebrija-Trejos et al. 2010). Therefore, ours and other studies show that the power of chronosequence models to predict short-term dynamics in successional forest may be site- or even

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**FIGURE 3.** Pairwise relationships between residuals from chronosequence models or net change models and site variables assessing management history, soil condition, and adjacent forest cover in secondary tropical dry forest (TDF) from the Chamela-Cuixmala region, western Mexico. Only those residuals and site variables significantly associated with ordination axis explaining them are shown; $P < 0.05$, Bonferroni corrected Spearman rank correlation tests). See Table 2 and text for further details.
attribute-dependent and should not be deduced from their explanatory power.

The possibility of a mismatch between chronosequences and dynamic approaches has potential implications for the application of the chronosequence approach to practical situations. For example, biomass and carbon stock recovery through succession in tropical forests is commonly inferred from forest structural measurements done along a chronosequence (Vargas et al. 2007, Yang et al. 2011, Becknell et al. 2012). As previously shown, however, net changes of structural attributes derived from chronosequences can be quite dissimilar from those observed through repeated measurements, making biomass and carbon recovery estimations significantly biased. Our findings therefore indicate the need for caution in the application of chronosequence data in evaluations of ecosystem service recovery.

Influence of Site Factors on Succession.—In our study, sites were selected to conform a chronosequence based on their location on similar biophysical conditions and to include the dominant field management features in the study region (Burgos & Maass 2004). Our results show, however, that variation in community dynamics is related to site factors, mainly those associated with field management previous to abandonment, even after accounting for the effect of age of abandonment. Such results suggest that field management history affects successional processes. In general, the higher residuals from net change models were associated with low extension or duration of field management and time since forest clearing (Fig. 3). An exception to this pattern was the higher residuals of the net changes model for richness found in sites where herbicide was applied. Thus, our results are in general concordance with previous findings about reduced successional recovery under more severe field management (Uhl et al. 1988, Moran et al. 2000, Zarin et al. 2005, Molina-Colon & Lugo 2006). An interesting implication of these results is the complexities involved in site selection for chronosequences: an assessment of management history is required to guarantee that sites have very similar management histories or, even better, that information is included during chronosequence data analysis. Further work is needed to more strongly support these findings by increasing sample size of plots and by including more contrasting field management conditions.

It is also interesting that both soil properties and adjacent forest cover did not show any association with the observed successional dynamics, although they were related to ordination axes-2 and 3. The limited contribution of soil conditions contrast with the sharp mosaic in geological origin found in the region (Cotler et al. 2002). Our results, though, concur with previous studies that showed that old growth TDF structure and diversity in the region is not affected by the type of geology and soil (Durán & Meave 2006), but rather by water availability, associated to the slope and position in the landscape (Balvanera et al. 2002). The lack of association between adjacent forest cover and model residuals could be explained by inadequate sampling or by the correlation between adjacent forest cover and age of abandonment. Our sample was not designed to test the effect of the surrounding landscape matrix features on site dynamics, so the lack of association could simply be the result of inadequate representation of the complete range of forest coverage around sites. On the other hand, we also found a significant correlation between age and forest cover, which we speculate could result from the spatial autocorrelation of management practices (Helmer et al. 2008, Crk et al. 2009). This correlation could imply that when testing the effect of age of abandonment, we may not only have tested the intrinsic processes of development of the forest, i.e., plant growth, but also the potential effect of extrinsic factors like increased seed rain and seedling establishment associated with increased adjacent forest cover, as has been previously shown (Maza-Villalobos et al. 2011).

Sample size limitations and performance of the analytical approach.—Our conclusions could be limited by the small sample size of the tropical dry forest dataset (nine secondary forest sites). Results from the analysis of these data, however, are consistent with the performance of the analytical approach under simulated conditions. NC exp trajectories observed for those community attributes with significant departure from expectations (basal area and mean height) are more consistent with a systematic departure of observed trajectories from chronosequence models than with a spurious effect caused by small sample size. Although small sample sizes caused a partial departure from chronosequence expectations during simulations, the analytical approach is relatively robust to sample size. Instead of causing the spurious rejection of chronosequence expectations, small sample size seems to be related to the reduced power of the test, since prediction intervals become wider as sample size reduces. On the contrary, simulations testing the effect of the degree of systematic departure between observed and expected NC show the test is sensitive to this parameter. Increased random deviation also results in higher divergence between observed and expected results (Appendix S2). Overall, simulations suggest that the analytical approach is sensitive to deviation in successional trajectories with respect to chronosequence model expectations.

We believe the analytical approach developed here has clear advantages beyond low sensitivity to sample size. Previous studies have tested the match between chronosequence and dynamic approaches by correlating predicted rates from a chronosequence model to observed rates (Maza-Villalobos et al. 2011). This constitutes a ‘coarse test’ of the chronosequence, since correlation can occur even when observed and expected rates show a different kind of relationship with time and, therefore, come from quantitatively different relationships between age and community attributes. In addition, correlations between age and observed rates do not actually test chronosequence predictions, as exemplified here by basal area, where the NCoVa were significantly related to fallow age, but the chronosequence model failed to predict them (e.g., Foster & Tilman 2000). Instead, our approach allowed us to test for specific predictions about expected community changes derived from specific statistical models fitted to community attributes. Its implementation in other chronosequence...
datasets will allow further assessments of its advantages and shortcomings.

CONCLUSIONS

We found that although age of abandonment has a high explanatory power for differences in community attributes of secondary TDFs, the predictive power of chronosequence models can be poor and not related to its explanatory power. Part of the mismatch between observed and expected net community changes over 6 yr may be caused by temporal environmental conditions affecting short-term successional dynamics, although differences in management history among sites could also influence such disparity. Our results point out the need to integrate chronosequence and dynamic approaches to better understand and predict secondary succession. Furthermore, they suggest that caution is needed when applying chronosequences to the evaluation of ecosystem services recovery. By providing an analytical approach to statistically test both the explanatory and predictive power of chronosequences, we have advanced in the integration of different approaches to study succession and, therefore, in the recognition of their possibilities and limitations.

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SUPPORTING INFORMATION

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

FIGURES S1 and S2. Expected net changes in attribute and their 95% CI limits in relation to age of abandonment.

FIGURE S3. Observed attribute net changes and the corresponding trajectory for the net change model.

FIGURE S4. Comparison between expected net changes predicted from chronosequence and those observed from dynamic data.

FIGURE S5. Simulation results for sample size variation.

FIGURE S6. Simulation results for variation in randomness of observed changes.

FIGURE S7. Simulation results for variation in the degree of systematic departure between observed changes and expected changes.

TABLE S1. Nonlinear models used to test the effects of age of abandonment on community attributes and their observed net changes for secondary tropical dry forests in abandoned cattle pastures and old growth forest sites in western Mexico.

TABLE S2. Site variables associated with ordination axes summarizing field management history, soil condition, and adjacent forest cover of secondary tropical dry forest woody communities in abandoned pastures in western Mexico.

APPENDIX S1. Analytic procedure to explore the power of chronosequences to explain and predict successional changes based on repeated measurements.

APPENDIX S2. Simulations for assessing the performance of the analytical approach to test chronosequence predictions based on the repeated measurements data.

APPENDIX S3. Site factors beyond age of abandonment explaining community attributes and observed net changes.

LITERATURE CITED


