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Predicted trajectories of tree community change in Amazonian rainforest fragments

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A great challenge for ecologists is predicting how communities in fragmented tropical landscapes will change in the future. Available evidence suggests that fragmented tropical tree communities are progressing along a trajectory of 'retrogressive succession', in which the community shifts towards an early or mid-successional state that will persist indefinitely. Here, we investigate the potential endpoint of retrogressive succession, examining whether it will eventually lead to the highly depauperate communities that characterise recently abandoned agricultural lands. We tested this hypothesis by using neural networks to construct an empirical model of Amazonian rainforest-tree-community responses to experimental habitat fragmentation. The strongest predictor of tree-community composition in the future was its composition in the present, modified by variables like the composition of the surrounding habitat matrix and distance to forest edge. We extrapolated network predictions over a 100 yr period and quantified trajectories of forest communities in multidimensional ordination space. We found no evidence that forest communities, including those near forest edges, were converging strongly towards a composition dominated by just one or two early successional genera. Retrogressive succession may well be stronger in fragmented landscapes altered by chronic disturbances, such as edge-related fires, selective logging, or intense windstorms, but in this experimental landscape in which other human disturbances are very limited, it is unlikely that forest edge communities will fully revert to the species poor assemblages observed in very early successional landscapes.

Habitat fragmentation induces rapid and strong changes to rainforest tree communities. For example, there is a loss of tree biomass (Laurance et al. 1997) spurred by elevated tree mortality, especially among larger trees (Laurance et al. 2000, Lindenmayer et al. 2012). There is also a proliferation of disturbance-adapted tree species (Laurance et al. 2006a, Tabarelli and Lopes 2008) and a loss of phylogenetic diversity (Santos et al. 2010). In a few years after isolation, newly created forest edges tend to 'seal' themselves with dense vegetation that reduces the microclimatic changes experienced within forest fragments (Didham and Lawton 1999). The long generation times of rainforest trees ensures that changes to floristic composition will take at least decades, and potentially even centuries, before a new equilibrium community is reached (Santos et al. 2010), if it is reached at all.

Such time lags make it difficult to determine the likely structure of future tree communities. Nonetheless, there is a lot of interest in understanding what the forests of the future may look like. Undisturbed tropical forests may represent a sizeable sink of atmospheric carbon (Phillips et al. 1998, Lewis et al. 2009), but habitat degradation around forest edges and in fragmented landscapes leads to increased emissions from standing forest (Laurance et al. 1998b, Numata et al. 2011, Chaplin-Kramer et al. 2015). Moreover, directional changes in forest composition from species with higher to lower wood density (Laurance et al. 2006a, Michalski et al. 2007) typically reduces the standing stocks of carbon in fragmented forests, although this trend is not universal (Ziter et al. 2014). Given the rapid rates of deforestation and forest fragmentation across the world's tropical rainforest biomes, and the important links among species composition, carbon storage and carbon emissions, it is important to try and predict the future composition of present-day forest fragments.

At least over the first few decades after isolation, most of the impacts of forest fragmentation on tree communities are driven by edge effects (Olupot 2009, Laurance et al. 2011, Benchimol and Peres 2015). Forest edges experience elevated wind turbulence (Somerville 1980, Laurance and Curran 2008) and altered microclimate conditions (Camargo and Kapos 1995, Chen et al. 1995, Didham and Lawton 1999, Ewers and Banks-Leite 2013) that are linked with increases in canopy dessication (Stevenson and Coxson 2008, Briant et al. 2010) and tree mortality (Chen et al. 1992, Brando et al. 2014, Badano et al. 2015, Hallinger et al. 2016), and those mortality rates increase even more for sites that are close to multiple edges (Laurance et al. 2006b). High mortality rates open canopy gaps and create opportunities for seedlings and saplings to recruit into the population, so it is no surprise that recruitment rates are also higher near forest edges than deep inside forest interiors (Chen et al. 1992, Laurance et al. 2006a, Bouroncle and Finegan 2011). The species traits associated with increased mortality and recruitment are non-random, with a set of slower-growing tree species with high wood density tending to decline in abundance whereas faster-growing tree and liana (woody vine) species with lower wood density are increasing (Laurance et al. 2006a, Pütz et al. 2011, Benchimol and Peres 2015). As a consequence, the turnover rate of species near forest edges is elevated (Laurance et al. 2006a), creating highly dynamic communities that are changing rapidly through time.

The trajectories of tree communities in fragmented landscapes are non-neutral (Gilbert et al. 2006) and may be approaching species compositions that are reminiscent of early successional communities (Tabarelli and Lopes 2008, Pütz et al. 2011). Tabarelli and Lopes (2008) and Santos et al. (2008) raised the hypothesis that fragmentation may drive tree communities through a process of 'retrogressive succession' and toward an early successional state that will persist indefinitely. Under this scenario, there will be no long-term community recovery from the initial disturbance of habitat loss and fragmentation, and the community will retain fewer species that are more commonly associated with regeneration sequences within forest gaps (Santos et al. 2008). This is a convincing hypothesis, with several studies demonstrating the proliferation of pioneer tree species near forest edges at the expense of shade-tolerant trees (Laurance et al. 2006a, b, Michalski et al. 2007, Santos et al. 2008, Benchimol and Peres 2015).

Here, we further refine the concept of retrogressive succession, recognising that the hypothesis could be tested in two ways: testing for convergence in the functional composition of the tree community with an emphasis on the traits of species; or testing for convergence in the taxonomic composition of the tree community with an emphasis on the identity of species. We believe there is ample evidence to support the functional trait version of the hypothesis (Laurance et al. 2006a, b, Michalski et al. 2007, Santos et al. 2008, Pütz et al. 2011), and instead focus our attention on the taxonomic version with the goal of determining the taxonomic endpoint of retrogressive succession. A full chronosequence of forest succession in fully cleared Amazonian landscapes begins with just one or two genera, typically *Cecropia* and/or *Vismia*, with the diversity of the successional community building through time until the slow-growing, shade-tolerant species are eventually able to establish themselves as dominant. Retrogressive succession has been shown to lead to a community composition dominated by a range of early and mid-successional tree and vine species (Laurance et al. 2006a, b, Santos et al. 2008, Tabarelli and Lopes 2008), but has not been linked to compositional changes so extreme as to generate the highly depauperate communities consisting of predominantly *Cecropia* and/or *Vismia* spp. that are observed at the start of the succession process.

The successional dynamics of tree communities are, however, slow and take many decades or centuries to fully manifest (Santos et al. 2008), whereas the longest-running set of continuous observations of tree-community dynamics following forest fragmentation encompasses just 35 yr (Laurance et al. 2011). It is possible, then, that given long enough time periods the process of retrogressive succession may accelerate, slow down or even reverse in the future. The increased mortality rates of shade-tolerant species near forest edges ensure it is improbable that edge communities will recover their pre-fragmentation composition, but continued dispersal from forest interiors to forest edges may render it unlikely that retrogressive succession will lead to the highly depauperate communities that are associated with early successional systems.

Here, we attempt to model the trajectories of tree-community change in Amazonian rainforest fragments, with a view to determining the long-term trajectory of community changes under retrogressive succession. We test the specific, falsifiable hypothesis that communities in small fragments and near forest edges will revert to the community composition observed in early successional systems. We use data from the Biological Dynamics of Forest Fragments Project (Lovejoy and Oren 1981, Laurance et al. 2011), taking advantage of the longest-running experimental dataset on tree-community responses to habitat fragmentation. We quantify observed, historical trajectories of change and then extrapolate them into the future, examining those trajectories to see if they result in communities that converge on community states that are characteristic of early successional habitats.

Testing hypotheses concerning future events

Our hypothesis can only be tested if we have a quantitative description of what the tree community in a fragmented landscape will look like one century following fragmentation, but the longest running experimental dataset that quantifies both pre- and post-fragmentation composition extends over just 25 yr (Laurance et al. 2006a). Our only option to test the hypothesis, then, is to simulate the community composition 100 yr into the future and conduct our hypothesis test on the simulation outputs. We have taken a three-step approach to this challenge.

First, we used ordination techniques to simplify a diverse tree community to its dominant gradients of community composition, and quantified observed changes in composition that have occurred over several decades (Lovejoy and Oren 1981, Laurance et al. 2011). Ordination allowed us to reduce a complex community dataset comprising several hundred genera to a handful of uncorrelated axes that summarise the patterns of covariation in genera composition. Thus we were able to model just the small number of multivariate axes and avoid the more problematic issue of modelling each of the hundreds of genera independently.

Second, we used neural networks to create a statistical, non-spatial model of community trajectories through ordination space that recreated empirically observed trajectories, and extrapolated those trajectories 100 yr into the future. Modelling the dynamics of species rich communities represents a tremendous challenge to ecologists (Purves and Pacala 2008, Perretti et al. 2013). Neutral models based on the Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001) can be used to examine the dynamics of tree communities in continuous forest, but fail to adequately capture the elevated rates of species turnover observed in fragmented forest (Gilbert et al. 2006). Individual-based models of tree growth, such as the FORMIX3 (Huth and Ditzer 2000) or perfect-plasticity approximation models (Purves et al. 2008), can be employed, but these require intensive parameterisation using species traits that are often unknown for the majority of tropical species. Thus we approach this problem by extrapolating trajectories of tree plots through ordination space using neural networks. Our approach is aspatial and statistical rather than explicitly based on a spatial model of the ecosystem processes that underlie the ecological patterns we are predicting. This approach lacks the detailed mechanistic understanding that would come from modelling the ecological processes underlying tree community changes directly, but comes with the advantage of allowing for highly non-linear interactions that can reproduce apparently 'erratic' dynamics (Ye et al. 2015). Non-linear dynamics are prevalent in our study system: previous analyses have demonstrated that forest dynamics here fluctuate markedly through time, and that they are acutely sensitive to local landscape and weather conditions (Laurance et al. 2007). Parametric and mechanistic models typically lack the flexibility to reproduce non-linear dynamics and have little predictive power compared to model-free forecasting approaches (Perretti et al. 2013, Ye et al. 2015), of which neural networks are just one examplar.

Third, we treated the simulated, 100-yr-in-the-future community as if it were observed community data and used those 'observations' to test our hypothesis. We quantified the multi-dimensional distance between the coordinates defining the location of successional genera in ordination space and the coordinates defining the location of plots at the beginning and end of the simulation. We used parametric statistics to test for convergence towards communities dominated by the successional genera. Statistical significance tests should be applied to simulation results with caution (White et al. 2014), but was appropriate for our analyses. We retained just one degree of freedom per vegetation plot and did not, therefore, artificially inflate the number of degrees of freedom in our significance tests (White et al. 2014), and because we have used equation-free neural networks the null hypothesis is not known to be false a priori by simple examination of model parameters (White et al. 2014).

Methods

Data collection

We used tree community data from the Biological Dynamics of Forest Fragments Project (Lovejoy and Oren 1981), collected from a 1000 km^2 area in central Amazonia. The dataset has been widely used and described elsewhere (Laurance et al. 2011). Importantly, the fragments in this study area have been protected from edge related fires, selective logging, hunting, fuelwood gathering, and other human disturbances that often affect other fragmented tropical landscapes (Laurance and Cochrane 2001). The fragments have also been fenced to prevent incursions of cattle. The experiment isolated nine forest fragments that range in size from one to 100 ha, and a total of 40 forest plots of 1 ha were distributed among the fragments ($n = 23$ plots) and in eight control sites ($n = 17$) in nearby continuous forest. All plots were sampled prior to fragmentation and have since been resampled at roughly 5-yr intervals. The data used here encompassed plots that were surveyed either three ($n = 7$ plots), four ($n = 19$), five ($n = 6$) or six ($n = 8$) times over a 25-yr period and are the same as presented by Laurance et al. (2006a). All individuals were identified at least to genus and this is the taxonomic level of our analyses. We chose to work at genus rather than species level because almost 90 % of tree species at this site are too rare for analysing individually, having < 1 individual per hectare, and because congeneric species tend to be ecologically similar in this study area (Laurance et al. 2004). There was a total of 267 genera represented in the dataset, with an average of 123 genera present in each plot.

Characterising tree communities and trajectories of change

Our goal was to quantify the trajectories of tree communities through time, so we required a quantitative ordination method rather than a semi-quantitative method such as the widely used non-metric multidimensional scaling (Legendre and Legendre 1998). We chose to use principal coordinates analysis (PCoA) that can work with any distance metric (Legendre and Legendre 1998). There are many distance metrics available to ecologists and the choice of metric can exert a strong influence on the results of ordination analyses (Legendre and Legendre 1998), so to determine the best distance metric for our purposes we compared the proportion of variance explained by PCoAs fitted using each of 13 different distance metrics as implemented in the R package 'vegan' (Oksanen et al. 2011). The Morisita distance metric explained the highest proportion of the variation in community composition and was therefore retained in all future analyses.

We used PCoA on a Morisita dissimilarity matrix to characterise the relative floristic composition of all plot × census observations. All plot × census combinations were entered into the same PCoA, ensuring trajectories of change in ordination space are comparable among time periods. To determine the appropriate number of ordination axes, we compared the distribution of explained variance among the ordination axes to the expected distribution of variance according to a broken stick model (Legendre and Legendre 1998). There were six PCoA axes that explained more variance than expected by chance and were retained in future analyses.

Neural networks, network averaging and network predictions

We used neural networks to explain observed, and predict future, changes in tree community composition. Neural networks were chosen for their ability to simultaneously fit non-linear models to multiple response variables. All neural networks were fitted using the R package 'neuralnet' (Günther and Fritsch 2010, Fritsch and Günther 2012).

We had six response variables in our neural networks, representing plot × census locations on the first six ordination axes from the PCoA described above. As predictors, we included the ordination values from the time step before, allowing for the fact that the best predictor of a plot's future state is likely to be its present state. We also used two metrics representing forest fragmentation, one being $\log_{10}$-transformed fragment area (sites in continuous forest were given an arbitrary area of 10 000 ha after Didham et al. (1998)), and the other being $\log_{10}$-transformed distance to nearest edge. We included the height of *Cecropia* and *Vismia* in the matrix habitat surrounding the fragment, as such regrowth near fragments can buffer edge effects and reduce edge-related tree mortality (Mesquita et al. 1999). *Cecropia* and *Vismia* dominate regrowth in the matrix surrounding forest fragments at the BDFFP, with the former dominant on soils that were not burned and the latter dominant on soils that were burned. Height was estimated as a function of time since fragmentation based on a growth model of central Amazonian secondary forests (Neeff and Santos 2005). Finally, we included the year of the plot survey to allow for temporal dynamics in large-scale environmental conditions such as regional climate that may impact all plots simultaneously (Laurance et al. 2014), and the number of years between plot censes (inter-survey internal) to allow for the fact that larger changes are expected to be observed over bigger time periods.

There are no formal guidelines on how to generate model-averaged predictions for neural networks, so we developed an approach consistent with approaches to model averaging used in parametric statistics. Model selection of a neural network must choose the optimal subset of predictor variables, as well as the optimal number of hidden nodes. Too few hidden nodes can mean the model does not have enough flexibility to capture nonlinearities in the data (Hastie et al. 2009), but too many hidden nodes can lead to overfitting and poor predictive performance (Lee 2001, Priddy and Keller 2005). We set an arbitrary range of hidden nodes with the minimum number being equal to the number of predictor variables in the network and the maximum to be five times the number of predictor variables, and fitted neural networks with all values between the minimum and maximum number of hidden nodes for each combination of predictor variables. All sets of predictor variables included the six ordination axes, to which we added all combinations of the six fragmentation and survey date variables. In total, we fitted 2343 separate network combinations (63 combinations of 12 predictor variables times a maximum of 60 hidden nodes).

We split the data into three, allowing us to independently train, validate and then test our network predictions (Hastie et al. 2009). First, we used data from the first three transition periods in the tree dataset for training and validating the model, randomly selecting 80% of these observations to use in model training and leaving 20% for model validation. The final two transition periods were retained for model testing. Because our goal was to use the neural networks for prediction, we used the sum of squared errors on the validation data set as a measure of network fit (Priddy and Keller 2005), thereby testing the ability of a fitted model to recreate patterns observed in a new dataset. Because the final network fit, and estimated network weights, might depend on which observations fell into the training and validation sets, we created a new random 80:20 split of the data each time a neural network was fitted. The final weights of a neural network can also depend on the initial starting values used, so we fitted each network three times using random starting values and a random data split, and recorded the sum of squares error calculated on the validation data set for each network fit. Not all network fitting attempts converged on solutions, and we attempted to obtain solutions a maximum of nine times per network combination. If none of the nine attempts converged, that network combination was removed from all future analyses.

Neural networks are often criticised for being a 'black box' approach to fitting models (Priddy and Keller 2005, Hastie et al. 2009), but it is possible to quantify the contribution of individual predictor variables to the final model fit using saliency scores (Priddy and Keller 2005). For each of the network combinations that we fitted, we calculated the saliency of each variable in the network. To obtain an average estimate of saliency, we first standardised the saliency scores for each individual network such that the sum of all scores was equal to one, and took the weighted average saliency score for each predictor variable across all models using the inverse sum of squares error as a measure of network fit as a weight. Thus predictor variables with high average saliency scores represent variables that make large contributions to neural networks that fit the data well.

To generate predictions of community change, we averaged the predictions arising from the set of best networks, defined as those that fell within 2 AIC points of the best-fitting network (Burnham and Anderson 2002). We predicted the new value of tree community composition for each forest plot, getting our final prediction by averaging the predictions arising from the set of best networks. To determine the accuracy of our predictions, we compared network predictions with the observed changes in our testing dataset, thereby accurately gauging our level of prediction error (Hastie et al. 2009). We had two 5-yr time periods represented in our testing dataset, effectively allowing us to test the accuracy of our models to make predictions over a 10 yr period.

Network predictions were iterated to simulate future trajectories of change for a 100 yr period. Static predictors in the model, such as fragment area and edge distance, were kept constant for each tree plot in each of the time steps of the simulation. Similarly, we specified a five-year census interval for all tree plots into the future. Dynamic predictors, such as the height of the matrix vegetation and PCoA scores, were updated at each time step. For example, the community composition observed at time 0 was used as a predictor for estimating community composition at time 1, and the predicted community composition at time 1 was used in turn to predict community composition at time 2, and so on.

Testing the end point for tree communities under retrogressive succession

We tested whether retrogressive succession will lead to tree communities near forest edges and in small fragments that are dominated by a limited number of early successional species. To do this, we took the six-dimensional coordinates of *Cecropia* and *Vismia*, the two genera that dominate recently abandoned land in these landscapes, and quantified the Euclidean distance in multi-dimensional ordination space between these two genera and plots at the beginning of the simulation, corresponding to their observed composition immediately prior to fragmentation, and at the end of the simulation, corresponding to their predicted composition 100 yr after fragmentation. We calculated the change in Euclidean distance for each plot, hereafter termed the 'convergence to succession'; negative values indicated plots that have communities predicted to converge towards the successional genera, while positive values indicated the opposite. Convergence to succession was calculated separately for the *Cecropia* and *Vismia* centroids, and used as a response variable in a multiple regression examining the influence of matrix type (*Cecropia*, *Vismia* or both), habitat fragmentation ($\log_{10}$-transformed distance to edge and $\log_{10}$-transformed fragment area), and their two-way interactions. The regression was run separately for convergence to each of the two successional genera. We expected to detect significant interaction effects between matrix type and habitat fragmentation, with plots located near forest edges or in small fragments and surrounded by a matrix of *Cecropia* should have trajectories tending toward the *Cecropia* centroid and vice versa for fragments in a matrix of *Vismia*.

Results

The first two axes of the PCoA explained 27 and 16% of the variation in community composition respectively, and the six significant axes explained a cumulative total of 83% of the variance. There were large changes in tree communities through time near edges (Fig. 1a). We fitted a total of 3843 neural networks, of which 1721 fell within 2 AIC points of the best model. Such a large number of models suggests there was little difference among neural networks in terms of their predictive power. Saliency scores demonstrated that the strongest predictor of community composition was composition in the time step before, with the six ordination axes selected as the six most salient variables across all fitted neural networks (Fig. 2). The height of *Cecropia* and *Vismia* in the matrix had intermediate saliency scores while fragmentation variables, such as fragment area and distance to edge, exerted relatively weak effects.

There was a very high correlation between observed and predicted values across all prediction intervals and ordination axes combined ($r_{130} = 0.96$, $p < 0.001$), and for both prediction intervals ($r > 0.94$, $p < 0.001$) and for all six ordination axes ($r > 0.93$, $p < 0.001$) separately. Linear regression between the observed and predicted values fitted a line with an intercept that did not differ from zero (intercept = –0.0002, SE = 0.0015, p = 0.87) but the slope differed from the 1:1 relationship (slope = 0.723, SE = 0.019; $p < 0.001$), indicating that the network predictions had a tendency to overestimate small observed values and underestimate large values (Fig. 3).

Extrapolating the neural networks 100 yr into the future predicted a slight tendency for plots in continuous forest and those located far from edges to converge in the first two axes of ordination space. By contrast, predictions for plots in small fragments and near edges had no consistent pattern of convergence (Fig. 1b), although we note that the neural networks were making predictions in six dimensions and the figure presents just two of those.

Network predictions provided little support for the hypothesis that retrogressive succession might lead to highly depauperate, early successional communities. Convergence to

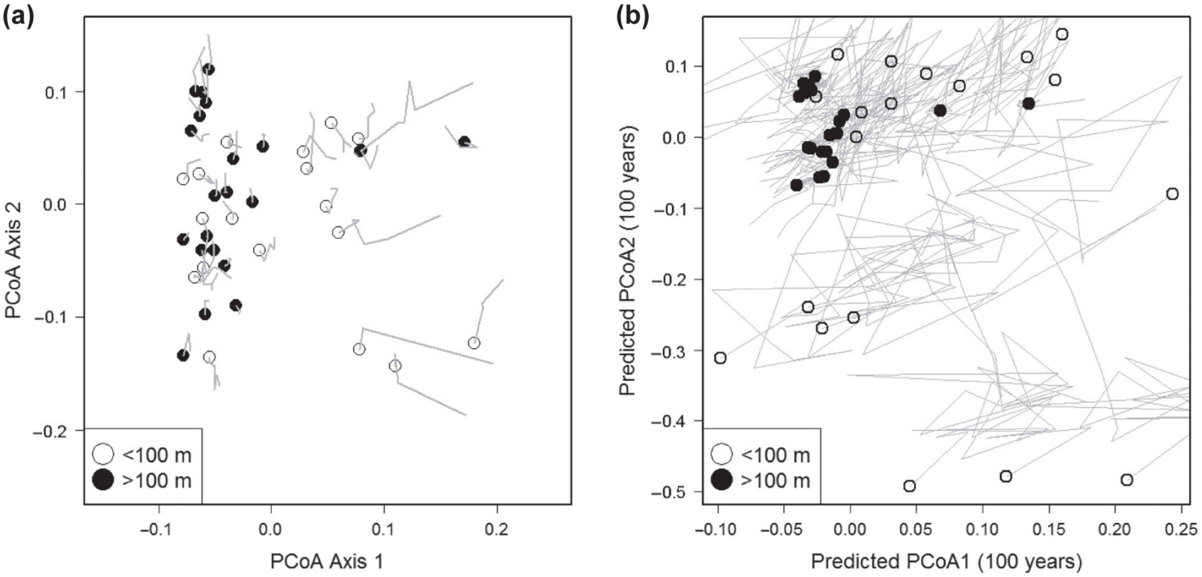

Figure 1. (a) The observed distribution of tree communities through time in ordination space over a 25 yr period. (b) Predicted locations of forest plots in ordination space 100 yr after fragmentation. Only the first two of six PCoA axes are plotted on both panels. Points in (a) show the composition of forest plots prior to fragmentation, with the temporal trajectory of each plot traced by a grey line that ends with the most recent observation (a) or with the predicted location after 100 yr (b). Symbols represent the distance to the nearest forest edge for each plot.

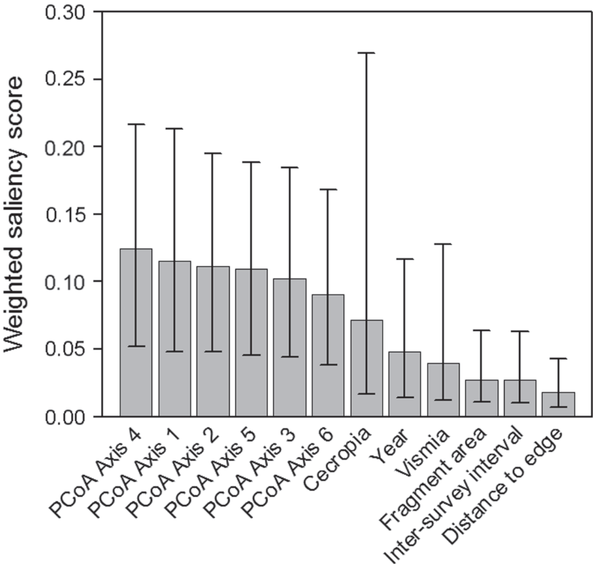

Figure 2. Median weighted saliency scores from 3843 fitted neural networks predicting tree community composition in a fragmented landscape. Bars represent median values and whiskers represent the 0.025 and 0.975 quantiles.

Vismia was negative for plots surrounded by a *Vismia* matrix whereas plots surrounded by *Cecropia* moved away from the *Vismia* centroid ($F_{2,31} = 34.0$, $p < 0.001$). However, the same pattern was also predicted for convergence to *Cecropia*, with plots surrounded by *Vismia* converging towards the *Cecropia* centroid and those surrounded by *Cecropia* diverging away ($F_{2,31} = 25.8$, $p < 0.001$). Both models had a significant interaction between matrix type and distance to edge (convergence to *Vismia*: $F_{2,31} = 7.28$, $p = 0.003$; convergence to *Cecropia*: $F_{2,31} = 9.78$, $p < 0.001$), but not in the expected direction. Plots far from edges showed little convergence in their distance to either *Cecropia* or *Vismia* regardless of matrix type, but plots near edges tended to diverge away from the *Cecropia* and *Vismia* centroids (Fig. 4).

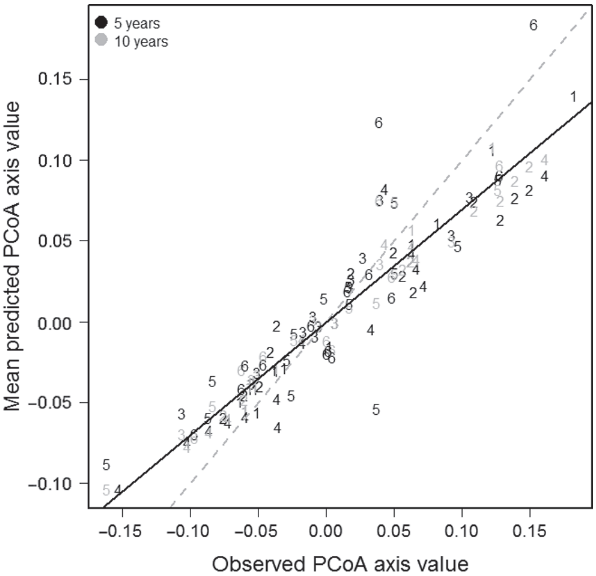

Figure 3. Prediction accuracy across a 10-yr period corresponding to two survey periods. The black line is fitted using linear regression through all points, and the dashed grey line represents the 1:1 relationship. Predicted values are the mean result from 1721 fitted neural networks. Points represent the locations of vegetation plots in six-dimensional ordination space, with numbers representing the six ordination axes.

Discussion

Predicting trajectories of biodiverse communities under global change represents a major challenge for ecologists and conservation biologists. It is already possible to do this in general terms, such as highlighting a tendency for animal-dispersed tree species (Harrison et al. 2013) and tree species with high wood density (Michalski et al. 2007), to decline in abundance in and fragmented defaunated forests. Statements like these are, however, highly qualitative and give little in the way of quantitative predictions. Numeric questions such as what proportion of species will decline *vs* increase in abundance, how large the abundance changes will be, and what the composition of future communities will be, remain unanswered. Here, we have attempted to make quantitative predictions of future community composition changes for an Amazonian rainforest tree community.

Neural networks represent a powerful new method for extrapolating trajectories of community change. Our approach of averaging predictions across many possible neural networks generated strong predictions of community change that accurately recreated observed trajectories of tree community change over a 10-yr period (Fig. 3). Moreover, equation-free modelling approaches have been demonstrated to generate more accurate predictions of future ecosystem states than parametric models based on the biology of species (Perretti et al. 2013, Ye et al. 2015). Parametric models themselves are often difficult to parameterise for diverse tropical communities where species traits are unknown for the majority of species, although there are notable examples where this has been achieved (Bohlman and Pacala 2012, Farrior et al. 2016). This gives us a basis for holding reasonable confidence in our ability to extrapolate community changes further into the future, although we recognise the inherent decline in prediction accuracy with increasing timeframes of the prediction.

We also highlight the limitations of using phenomenological models – such as the equation-free neural network approach we employed – over the use of mechanistic models that attempt to recreate the ecological processes that generate community changes (Huth and Ditzer 2000, Gilbert et al. 2006, Purves and Pacala 2008). Mechanistic models do not, as yet, have the predictive power of phenomenological, equation-free approaches (Perretti et al. 2013, Ye et al. 2015), but the predictions arising from phenomenological models have limited utility if the underlying processes determining community trajectories change in the future. We see the development of better mechanistic models that are able to more accurately predict the composition of forests over hundred-year timeframes as an exciting, and important, challenge for forest ecologists.

Using our phenomenological models, we found that community composition in the future is best predicted by community composition in the present, with the fragmentation variables of fragment area and distance to edge appearing to have relatively weak influences on community trajectories (Fig. 2). This stands in apparent contrast to a large literature that emphasises the impacts of habitat fragmentation on community changes (Laurance et al. 1998a, 2006a, Hill and Curran 2005, Santos et al. 2008, Tabarelli and Lopes 2008, Olupot 2009, Briant et al. 2010, Bouroncle and Finegan 2011, Pütz et al. 2011, Benchimol and Peres 2015). We stress, however, that the relatively weak effects of fragmentation variables does not imply that they are weak determinants of community change in these fragmented landscapes. Rather, in any given time step of just five years, the low number of mortality and recruitment events relative to the number of individuals who survive for a five-year period ensures fragmentation variables are not strong enough to result in complete turnover of tree communities. Fragmentation variables, therefore, do not override the dominant influence of the pre-existing community composition over short time scales such as the five-year census intervals in our data, but over long time scales fragmentation clearly influences the direction and magnitude of community changes (Laurance et al. 2006a).

Our network predictions found that composition of the surrounding matrix of modified habitats influenced the trajectories of community composition within fragments, in line with previous studies that found matrix composition influences the tree species being recruited inside forest fragments (Nascimento et al. 2006, Chabrerie et al. 2013, Benitez-Malvido et al. 2014, Aragon et al. 2015) and on the composition of fragment communities more widely (Brudvig et al. 2017). On average, matrix type exerted a slightly higher influence than distance to edge and fragment size (Fig. 2), but more detailed analyses of trajectories demonstrated that communities near forest edges were not predicted to converge towards communities dominated solely by the dominant successional genera *Cecropia* and *Vismia* (Fig. 4). Instead, our model predictions reinforced previous analyses of these datasets that have shown that the trajectories of change among edge communities appear inconsistent (Laurance et al. 2007), united only by the fact that their composition diverges away from that of continuous forest (Collins et al. 2017). One possibility to explain this is the landscape divergence effect (Laurance et al. 2007), in which small differences in starting conditions can result in large differences to the observed impacts of forest fragmentation on communities. Our finding that present-day community composition is the strongest and most consistent predictor of future composition supports this, and opens the possibility that forest fragmentation may influence tree communities very differently depending on their composition prior to fragmentation. New experiments, such as the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysia (Ewers et al. 2011), present an opportunity to test this hypothesis more widely and across a wider range of taxa.

Perhaps because of the landscape-divergence effect, we found little support for the hypothesis that retrogressive succession will drive forest-edge communities to an early successional state. We stress that this should not

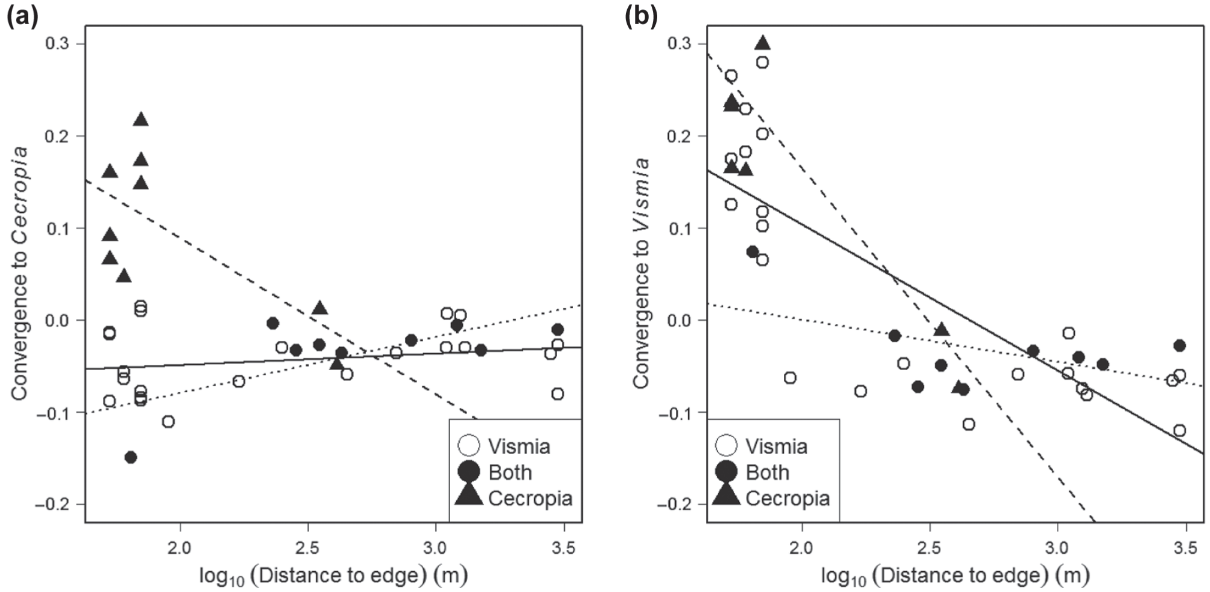

Figure 4. The role of distance to forest edge and matrix type on predicted trajectories of community composition over a 100 yr time frame. Values on the y-axis represent convergence (negative values) or divergence (positive values) of communities in multivariate space towards the successional genera *Cecropia* (a) and *Vismia* (b). If retrogressive succession leads to the highly depauperate communities observed in early successional landscapes, we would expect to see in panel (a) that plots with *Cecropia* in the matrix, either alone (dashed line) or in combination with *Vismia* (solid line), would have a positive slope indicating plots near forest edges converge towards the multidimensional centroid for the genus *Cecropia*; and in panel (b), that plots with *Vismia* in the matrix, either alone (dotted line) or in combination with *Cecropia* (solid line), would have a positive slope indicating plots near forest edges converge towards the multidimensional centroid for the genus *Vismia*.

be considered a rejection of the retrogressive succession hypothesis itself, for which we believe there is ample evidence. Rather, we have explicitly tested whether retrogressive succession is driving the taxonomic composition of the tree community towards the highly depauperate composition of early successional habitats. Moreover, we have used a highly conservative definition of early successional habitat that emphasises the dominance of two successional genera, ignoring within-genus variation in functional traits and the proliferation of other successional genera such as *Inga* spp. These limitations preclude us from testing for more mild forms of retrogressive succession that might lead communities to converge on mid- or late-successional stages that have a higher diversity of pioneer species. Second, our analysis has solely explored the retrogressive succession hypothesis in the context of taxonomic composition, and we make no claim about accepting or rejecting the hypothesis with respect to the potential convergence of functional traits that has been examined by other work at this study site (Laurance et al. 2006a, b) and elsewhere (Michalski et al. 2007, Santos et al. 2008, Tabarelli and Lopes 2008, Pütz et al. 2011, Benitez-Malvido et al. 2014). Third, the forest fragments we studied are experimental in nature, square (rather than irregular) in shape, isolated by only limited distances (70–800 m from intact forest), and are nearly free of other anthropogenic disturbances such as edge-related fires, selective logging, hunting, and fuelwood gathering that plague many fragmented landscapes in non-experimental contexts (Laurance and Cochrane 2001, Haddad et al. 2015). This latter caveat could clearly have a major influence on our findings, and there is good evidence that fragments in some human-dominated landscapes do in fact suffer much heavier degradation than do those at the BDFFP (Viana et al. 1997, Laurance and Cochrane 2001, Laurance and Williamson 2001, Santos et al. 2008, Schnitzer and Bongers 2011, Brando et al. 2014).

Communities near edges and in small fragments did not begin to converge towards a composition dominated by the two genera that characterise succession in this landscape over a modelled 100-yr period, regardless of the matrix type surrounding the fragments. This was a surprise, particularly given the known increase in abundance of both *Cecropia* and *Vismia* within the tree communities themselves that has occurred post-fragmentation (Laurance et al. 2006b, Nascimento et al. 2006). We suggest this apparently contradictory result arises because the proliferation of these two genera is merely symptomatic of a broader change in community composition, of which changes in *Cecropia* and *Vismia* abundance are just one component. Recent analyses have demonstrated that even in continuous forest, Amazonian tree communities are changing towards one that has a heavier bias to more closely related, fast growing species typical of mid-successional stages (Santos et al. 2014). Clearly, over long time scales, tree communities in fragmented landscapes are changing from being dominated by slow growing, shade tolerant, high wood density species to faster growing, light loving, low wood density species that are characteristic of treefall gaps and mid successional vegetation (Laurance et al. 2006a, Michalski et al. 2007, Santos et al. 2008, Pütz et al. 2011). However, the diversity of successional species observed in plots at forest edges exceeds the diversity of successional species observed in recently abandoned matrix habitats. So, while it is reasonable to characterise communities as changing towards one that is reminiscent of successional communities and that is dominated by species that have functional traits associated with successional communities, we do not believe these communities will collapse into the heavily depauperate communities comparable to the earliest stages of forest succession on abandoned land.

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