

VOLUME II

**ISOLATED *FICUS* TREES AND CONSERVATION
IN HUMAN-MODIFIED LANDSCAPES**

Chapter 9 to Appendix 5

CHAPTER 9:

Are isolated fig trees the “living dead”?

9.1 Preface

Wherever studied, isolated trees in human-modified landscapes around the world are expected to continue to decline in the coming decades. Given the importance of isolated *Ficus* trees to conserving the composition and structure of ecological communities in Assam, this chapter investigates whether *Ficus* trees in the study area are likely to share that common fate.

Authors: H. Eden W. Cottee-Jones, Philip Gibbons, Thomas J. Matthews, B. Dhanya, Robert J. Whittaker

The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J, BD. Analysed the data: HEWC-J, PG. Wrote the paper: HEWC-J, PG, TJM, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

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9.2 Abstract

Scattered *Ficus* trees (Moraceae) are critically important ecological elements of human-modified landscapes in the tropics. However, in all landscapes studied, scattered trees are predicted to decline markedly over the next century. We gathered data on the current density, regeneration periods, growth, recruitment, and mortality rates of two widespread *Ficus* species in Assam, India, to parameterise a population simulation model. Using 300 Monte Carlo simulation runs over 300 years, we predict an increase in the density of *F. benghalensis* of 19.79% by 2313, and an increase in *F. religiosa* by 11.40% over the same period. However, when accounting for uncertainty in our model, the population density in 300 years is likely to be similar to current densities. Predictions for both species were most sensitive to changes in mortality. Stress tests indicated that both populations were particularly vulnerable to changes in mortality, and to scenarios with a combination of high mortality and low recruitment. Although it appears likely that scattered *Ficus* trees will persist over long time scales in this landscape, we recommend that efforts to minimise adult mortality and maintain conditions for natural recruitment are critical, especially as these trees may serve crucial roles in providing ecological connectivity in the region via seed dispersal and gene flow.

Keywords Assam, *Ficus*, India, mortality, recruitment, scattered trees, simulation model, sensitivity analysis, stress test

9.3 Introduction

Ficus trees (Moraceae) are critically important components of forest ecosystems throughout the tropics (Corner, 1962; Terborgh, 1986; Lambert, 1989; Bleher et al., 2003; Tello, 2003; Kinnaird & O'Brien, 2005). The high volume of fruit (Korine et al., 2000), which is often produced in times of general fruit scarcity (Terborgh, 1986), along with the unusually high concentrations of rare minerals (O'Brien et al., 1998; Wendeln et al., 2000), makes *Ficus* trees important food resources for many frugivorous mammals and birds (Shanahan et al., 2001). The interaction with frugivorous species is a major driver of seed dispersal in tropical forests, and helps to determine the composition and relative abundances of plant communities (Howe & Smallwood, 1982; Howe & Miriti, 2004). Beyond forests, in human-modified landscapes, there is increasing evidence that this relationship remains intact, with reports of a high diversity and abundance of frugivorous birds visiting networks of scattered *Ficus* trees (Eshiamwata et al., 2006; Caughlin et al., 2012; Cottee-Jones et al. *in review*). Importantly, the persistence of this interaction helps conserve seed dispersal mechanisms, with scattered *Ficus* trees attracting a higher rate and diversity of seed rain, along with richer and denser sapling understories, than other scattered trees (Guevara & Laborde, 1993; Slocum, 2001; Guevara et al., 2004; Cottee-Jones et al. *in review*). The conservation of networks of scattered *Ficus* trees may therefore help conserve ecological functions such as seed dispersal and tree recruitment. However, the future of the scattered *Ficus* populations themselves also needs to be safeguarded.

In many human-modified landscapes around the world, scattered trees face a regeneration crisis, where high mortality coupled with low recruitment are predicted to cause major declines in scattered tree densities over the next 100 years (Manning et

al., 2006; Gibbons et al., 2008; Fischer et al., 2010). Reasons for these declines include natural senescence (Gibbons & Boak, 2002; Sherren et al., 2010), early mortality through elevated nutrient loads (Landsberg et al., 1990), salinity (Kimber, 1981), desiccation (Laurance et al., 2000), soil compaction (Yates & Hobbs, 1997), human clearance (Freudenberger & Ozolins, 2000; Ozolins et al., 2001), disease (Brasier, 2001), or low recruitment (Pulido et al., 2001; Hanspach et al., 2011; Harvey et al., 2011), which is often a function of the same problems driving early mortality, with the addition of high grazing pressure and competition with ruderal grasses (Holl et al., 2000).

In addressing the scattered tree regeneration crisis, several studies have highlighted the importance of increasing recruitment rates (Harvey & Haber, 1999; Plieninger et al., 2004; Vesk & Dorrough, 2006; Le Roux et al., 2014) and reducing mortality rates in mature trees (Gibbons et al., 2008). In the absence of management strategies that address both issues, scattered trees in human landscapes may in fact be the fast disappearing “living dead” (sensu Janzen, 1988; Manning et al., 2006).

Along with the threats faced by scattered trees in general, scattered *Ficus* trees face additional challenges. Due to their mutualistic relationship with pollinator fig wasps (Hymenoptera) (Compton et al., 1994), models predicting the minimum population of *Ficus* trees needed for a 99% probability of persistence over 1,000 years suggest an effective population size ranging between 170–2,000 *Ficus* trees may be needed, depending on the degree of seasonality (Anstett et al., 1997). Even if *Ficus* trees occur at moderate densities, protected areas may not be large enough to sustain viable populations without effective networks of *Ficus* trees in the intervening human-modified landscapes (Mawdsley et al., 1998; Nason et al., 1998; Walker, 2007).

To assess the prospects of *Ficus* tree populations in a human-modified landscape, we simulated changes in the density of two *Ficus* species, *F. benghalensis* and *F. religiosa*, using a modified version of an established scattered tree simulation model (Gibbons et al., 2008). In particular, we sought to investigate: 1) how the population densities of the two *Ficus* species were predicted to change over long time periods under current conditions; 2) how sensitive *Ficus* tree densities were to particular input variables; 3) how resilient would *Ficus* tree densities be to deteriorations in recruitment and mortality rates?

9.4 Methods

9.4.1 Study area

Fieldwork was conducted between October 2012 and June 2013 in the Golaghat District of Assam, North-eastern India (Figure 9.1). The study site was a ≈ 250 km² area bounded by the Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93 54.978. The study area is 30–100 m above sea level, and the mean annual rainfall for the region is 1,500–2,500 mm, most of which falls in the May to August monsoon (Barua & Sharma, 1999; Shrivastava & Heinen, 2007). The annual temperature range varies from an average minimum of 5°C to an average maximum of 35°C (Barua & Sharma, 1999).

The original habitat of moist subtropical deciduous forest was largely cleared following the local commercialisation of tea production in 1840 (Shrivastava & Heinen, 2007). Remnants of the original forest remain in the 7.65 km² Panbari Forest Reserve on the edge of the Karbi Hills, and in the 430 km² Kaziranga National Park (Barua & Sharma, 1999). The landscape is an agricultural mosaic, with a

heterogeneous assortment of smallholder rice cultivation, tea estates, and village home gardens. The area has a population density of 302 people/km² (GOI, 2011).

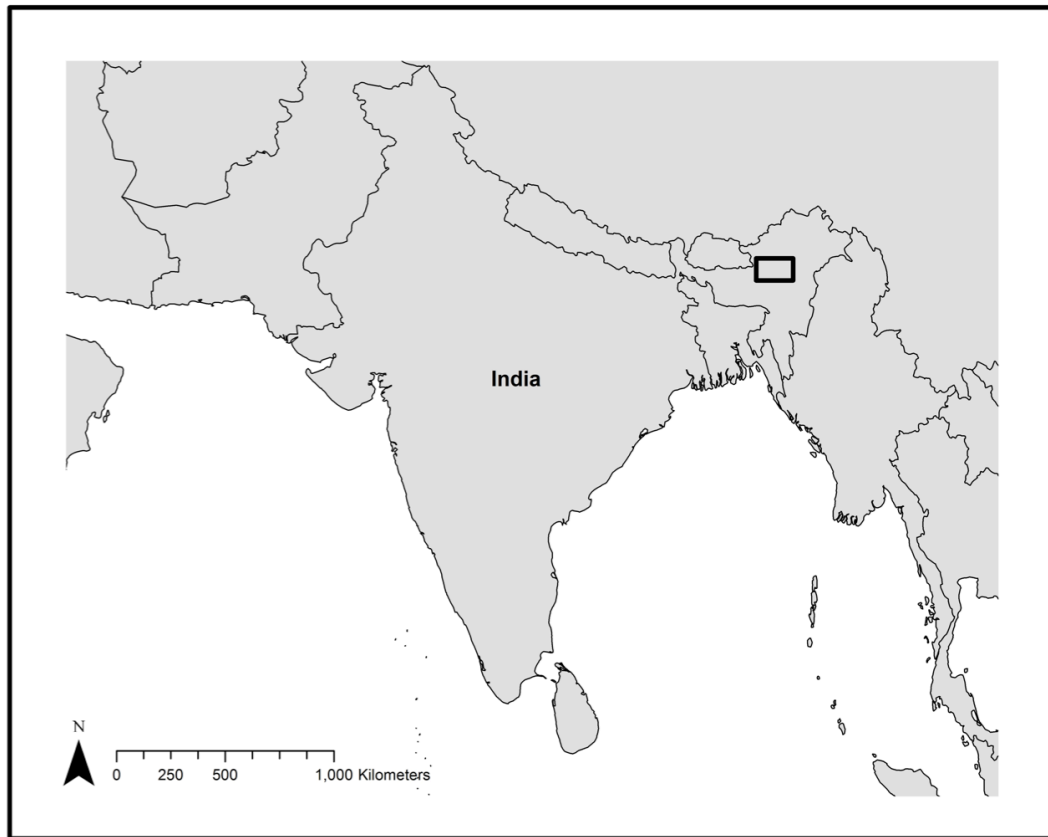


Figure 9.1: Map of South Asia, with the location of the study area indicated by the black box.

9.4.2 Population simulation model

To predict changes in the future density of isolated *Ficus* trees in the study area, we adapted an established simulation model that has previously been used to predict the rates of tree declines in eight landscapes around the world (Gibbons et al., 2008; 2010; Fischer et al., 2010; Manning et al., 2013; Le Roux et al., 2014). The model tracks the mean diameter at breast height (DBH) of trees in separate size cohorts over time. For this study, the model was parameterised with the initial density of *Ficus* trees across the study area, the predicted age and growth rate of trees, isolated *Ficus*

tree mortality rate, maximum *Ficus* age, recruitment periods, and the density of saplings recruited at each recruitment event (Table 9.1). We confined our simulation models to the two most abundant species in the study area, *F. benghalensis* and *F. religiosa*, as these were the only species for which we had adequate sample sizes for model parameterisation.

Table 9.1: The variables used to parameterise the *Ficus* population simulation model, and the values used to generate random numbers for the Monte Carlo runs. Means and standard deviations (SD) were estimated using the methods described in the second column, and were then used to discretise normal distributions for the generation of 300 random numbers, one for each Monte Carlo run. In the case of the density of recruits, a Poisson distribution was used, as these figures were derived from count data. In cases where the random number generation produced scores that were biologically or ecologically impossible (such as negative growth scores), these scores were converted to zero.

Variable	Estimation	Means±SD used for <i>F. benghalensis</i>	Means±SD used for <i>F. religiosa</i>
Current density of <i>Ficus</i> trees	Estimated by mapping the mature <i>Ficus</i> trees in the study area, and entered into the model after dividing trees of both species into 0.5 m DBH cohorts.	0.46 trees/km ²	0.94 trees/km ²
Maximum tree age	Estimated from reports in the non-academic literature and parameterised in a normal distribution with wide standard deviations.	250±50 years	250±50 years
Rate of tree growth	Coefficient for DBH in our linear regression model used to predict tree age. Linear regression models were fitted separately for both species. Values were drawn randomly from a normal distribution, negative values were converted to 0.	11.20±16.42	16.95±14.55
Density of recruits	Estimated separately for each species with the DISTANCE program, using data on the number of saplings recorded during transects in three land-use types. Values were drawn randomly from a Poisson distribution.	7.43±3.92	11.47±4.52

Recruitment period	Our regression model indicated that both <i>Ficus</i> species took eight years to reach 0.5 m DBH, which is the smallest DBH cohort included in the model, and 16 years to reach 1.0 m, which is the upper bound of that cohort. Recruitment frequency was therefore estimated to be 8–16 years, with values drawn randomly from a uniform distribution for use in the model.	8–16 years	8–16 years
Annual mortality rate	Fixed proportion of trees that die each year, calculated by $1-s^{(1/y)}$, where s is the proportion of trees that survive from one cohort to the next, and y is the number of years it takes to progress from one cohort to the next by 0.5 m DBH increments. Values were drawn randomly from a normal distribution, and negative values were excluded.	0.07±0.10	0.06±0.07

9.4.3 Current *Ficus* density estimation

To estimate the current density of *Ficus* trees in the study area, we conducted a thorough search of the landscape by car and on foot. We marked each mature *Ficus* tree with a GPSmap 62s device, typically accurate to ≤ 5 m in the open habitats the *Ficus* trees were situated. The most common *Ficus* species encountered were *F. religiosa* and *F. benghalensis*, followed by *F. rumphii*, *F. racemosa*, *F. microcarpa*, *F. assamica*, and *F. benjamina*. As *F. assamica* only grew to the height of a shrub, it was excluded from the mapping exercise. We recorded the land ownership (public or private) for each tree, and noted whether it was growing within 10 m of the roadside. Where the trunks were accessible, we measured the DBH (at 1.37 m above ground level) for these trees. In cases where trees had multiple support trunks, we only measured the largest stem. Trees were judged to be mature if they had a DBH > 0.5

m, as this was the DBH of the smallest tree that produced fruit in a parallel fruit monitoring study (Cottee-Jones et al., *in review*).

Once the mapping exercise was completed, we uploaded the *Ficus* locations into ArcGIS 10.2 (ESRI, 2014), and overlaid them on Landsat 8 satellite images of the study area. After placing 1 km² grids over the study area, we identified 202 grids where our survey effort had been comprehensive (in which we conservatively estimate that $\geq 90\%$ of the mature *Ficus* trees were discovered). For these grids, we recorded the dominant land-use cover, and counted the number of mature *Ficus* trees growing in each. We averaged the densities of all *Ficus* trees in these grids to estimate the overall mean density of mature *Ficus* trees per km² in the study area. To provide input data for DBH cohort sizes, the density of *F. benghalensis* and *F. religiosa* trees in each 0.5 m DBH cohort was calculated for a 125 km² plot where we had very high DBH measurement coverage (81.82% of all mature *Ficus* trees that were found were measured) (Figure 9.2).

9.4.4 Growth rate estimation

To estimate the growth rates of *F. benghalensis* and *F. religiosa*, we used data on DBH and landowners' tree age reports gathered for these species in a similar agricultural landscape from Karnataka, India (Dhanya et al., 2013). Although differences in rainfall between Karnataka and Assam suggest that our growth rate estimates may be conservative, this was the only known dataset which could provide tree age estimates for our study species in a non-forest setting. We established a relationship between DBH and tree age for each species using linear regression models to predict tree age from DBH (Table 9.2). To account for uncertainty in growth rates in the model inputs, we generated 300 random numbers within a defined normal distribution for each species using the `rnorm` function in R (R Core Team,

2014). Although a discretised normal distribution gave the best fit to observed parameter values, on rare occasions the random draws would return a negative number, which we converted to 0 (Anstett et al., 1997). We used the growth coefficients estimated by the regression model as the means for each species, and converted the coefficient standard errors into standard deviations to discretise the normal distribution.

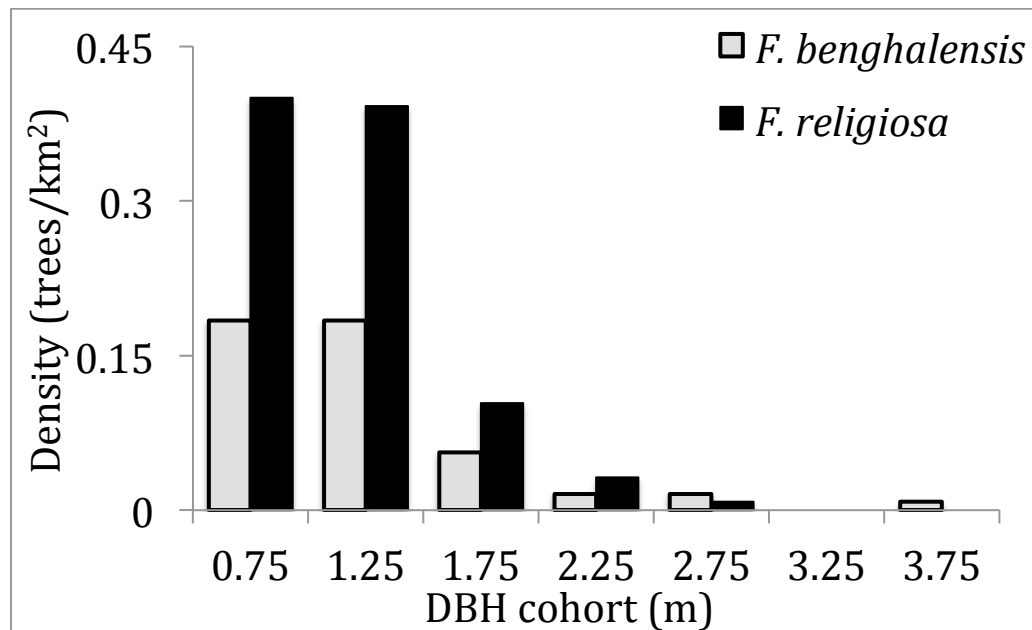


Figure 9.2: Frequency of tree occurrence in 0.5 m DBH (diameter at breast height) cohorts, for mature *F. benghalensis* and *F. religiosa* trees in a 125 km² part of the study area in Assam, India. X-axis categories are the median of each cohort, so that “0.75” refers to trees with a DBH of 0.5–1.0 m.

Table 9.2: The intercept, coefficient, adjusted R^2 and p value for the linear regression models fitted to predict tree age (in years) from diameter at breast height (in m) for two species of *Ficus* tree.

Species	Intercept	Coefficient±SE	Adj. R^2	p
<i>F. benghalensis</i>	4.12	11.20±1.79	0.32	<0.001
<i>F. religiosa</i>	-8.57	16.95±2.53	0.59	<0.001

9.4.5 Mortality rate estimation

The mortality rate for the two *Ficus* species in our study area was estimated from the proportion of individuals that survived from one DBH cohort into the next (DBH cohorts were classified in 0.5 m categories, starting with 0.5–1.0 m), with negative values converted to zero. As trees were isolated in the landscape, rather than growing in forest stands, we used a non-density dependent fixed rate of annual mortality. Therefore, for each species, we averaged the proportion of individuals that survived from each cohort across all cohorts. The mortality rate was estimated by the equation: $1-s^{(1/y)}$, where s is the mean proportion of trees that survive from one cohort to the next, and y is the mean number of years it takes to progress from one cohort to the next by 0.5 m DBH increments (Gibbons et al., 2008). We generated 300 random numbers from a normal distribution using our estimated mean annual mortality and standard deviations for each species for our 300 model runs using the `rnorm` function.

9.4.6 Maximum age estimation

There is little academic literature recording the maximum age of *Ficus* trees, although one *F. religiosa*, known as the “Bodhi Tree”, is believed to be 2,500 years old (Chandrakanth et al., 1990; Wilson & Wilson, 2013). We treat this record as the exception, and note that most estimates (sourced in non-academic literature) suggest that the oldest *F. benghalensis* and *F. religiosa* trees are 200–400 years old (Cottee-Jones et al., *in review*). Given the lack of reliability in these estimates, we conservatively used a maximum age of 250 years for both species. We used this figure as the mean maximum age, with a standard deviation of 50, to generate a range of random values for our simulation models using the `rnorm` function. While the paucity of available data to support this estimate may constrain the reliability of our

model, previous studies indicate that long-term predictions of tree density changes are not sensitive to uncertainty in this variable (Gibbons et al., 2008).

9.4.7 Recruitment estimation

To estimate recruitment rates for the two species, we ran 10 km transects through each of the three dominant land-use types in our study area: tea estates, paddy fields, and village home gardens. Transects were conducted from the back of a slow moving open-top jeep, with two observers spotting *Ficus* saplings growing either on the ground or epiphytically on trees or buildings. Saplings were defined as young trees between 20 cm and 10 m tall – this upper limit was just below the height of the shortest fruit-bearing *Ficus* tree we recorded in a parallel study (12.74 m, DBH= 0.5 m; Cottee-Jones et al., *in review*), and corresponded to 0.5 m DBH in the growth rate models for both species. The species, distance along transect, and perpendicular distance from the transect line were measured (using a 50 m tape measure) and recorded for all saplings. In 62.37% of cases, the sapling was growing high up in a host tree, and so the height (from the rooting point to the highest branch tip) had to be estimated. We estimated the density of *F. benghalensis* and *F. religiosa* saplings in the three land-use types with the DISTANCE program (Version 6.0; Thomas et al., 2010), using 5% right truncation and the minimum Akaike's Information Criterion to select the model with the best fit (Burnham & Anderson, 2002). We stratified the density estimate by the extent of each land-use type in the study area, and then calculated a mean sapling density estimate for both species. As the recruitment estimates were based on count data, we used a Poisson distribution, with a defined lambda (taken as the mean seedling density estimated above, for each species), to generate random recruitment densities for our simulations.

In the absence of data on *Ficus* recruitment period (the length of time an established *Ficus* seedling takes to reach maturity), we calibrated the uncertainty in recruitment intervals by taking a range of values derived from our tree growth regression models, where both species took eight years to reach the smallest DBH size included in the model (0.5 m), when the intercept was fixed at 0. Both species also took 16 years to reach the upper bound of this DBH cohort (1.0 m), and so to quantify uncertainty in the frequency of recruitment, we randomly generated numbers from a uniform distribution with a defined range (8–16 years).

9.4.8 Model parameterisation

Parameterised with the data described above, we used our simulation model to predict changes in the mean densities of mature *F. benghalensis* and *F. religiosa* trees over time in our study area. The initial densities of the two species in each DBH cohort were those calculated during our DBH measurement exercise, as illustrated in Figure 9.2. Simulations were conducted over 300 years using a Monte Carlo simulation with 300 model runs. This approach requires random sampling over multiple simulations to generate heuristic probabilities (McCarthy et al., 1995). Therefore, for each run of our model, input data on annual mortality rate, tree growth rate, and maximum age were drawn randomly from a normal distribution with means and standard deviations derived from our estimates, while data on the density of recruits at each time step were drawn randomly from a Poisson distribution, and recruitment periods from a uniform distribution, as described above. To assess changes in density over the period modelled, we compared average tree densities over the first and last 10 model intervals because of the discrepancy between our year 0 data and modelled data, which was caused by fairly weak tree growth models. To express uncertainty in our

predictions, our results are presented as means \pm 95% prediction interval (PI), following the formula provided in Gibbons et al. (2010).

9.4.9 Sensitivity analysis

We performed a sensitivity analysis to identify variables that can be manipulated to influence *Ficus* density patterns in the future. We used a hierarchical multiple regression model to examine the relationships between the mean predicted density of mature *Ficus* trees/km² of each species after 300 model runs and the potential explanatory variables: mortality rate, recruitment rate, growth rate, recruitment period, and maximum age. In both cases, the dependent variable was logarithmically transformed ($\text{Log}_{10}[x+1]$), and the standardised residuals were plotted against theoretical quantiles in a Normal Q-Q plot, to meet and check the assumption of normality. As p values are inappropriate for model selection using simulated data, we calculated the effect size using Cohen's f^2 to identify the most sensitive parameters in the model (Le Roux et al., 2014).

9.4.10 Scenario modelling

We investigated the potential impacts of manipulating variables that could be influenced by land management actions on *Ficus* population densities by conducting three “stress tests” per species. Here we adapted the definition of a financial stress test (Blaschke et al., 2001), so that an ecological stress test is “an analysis conducted with unfavourable environmental scenarios that are designed to determine whether a population can withstand the impacts of adverse developments”. The three scenarios tested were: 1) lower *Ficus* recruitment rates; 2) higher *Ficus* mortality rates; 3) lower recruitment and higher mortality rates. We used the lowest recruitment rates and highest mortality rates as simulated by the random number generation for the original

status quo models as the means for the stress tests, and used the same standard deviations as originally estimated. The annual mortality rate values used were 0.29 ± 0.04 (mean \pm SD) for *F. benghalensis*, and 0.05 ± 0.01 for *F. religiosa*; and the density of recruits was $2 \pm 3.92/\text{km}^2$ for *F. benghalensis* and $4 \pm 4.52/\text{km}^2$ for *F. religiosa*. Variables that could not be manipulated by management actions (recruitment period, growth rate, and maximum age) were fixed at their mean estimated values as determined for the original models. We ran 100 simulations for each scenario. In all simulated stress tests, changes in recruitment and mortality were assumed to take effect immediately. The simulation model was built and run in Excel using Visual Basic, and where not already specified, the statistical analyses were completed using SPSS 22 (IBM, 2013).

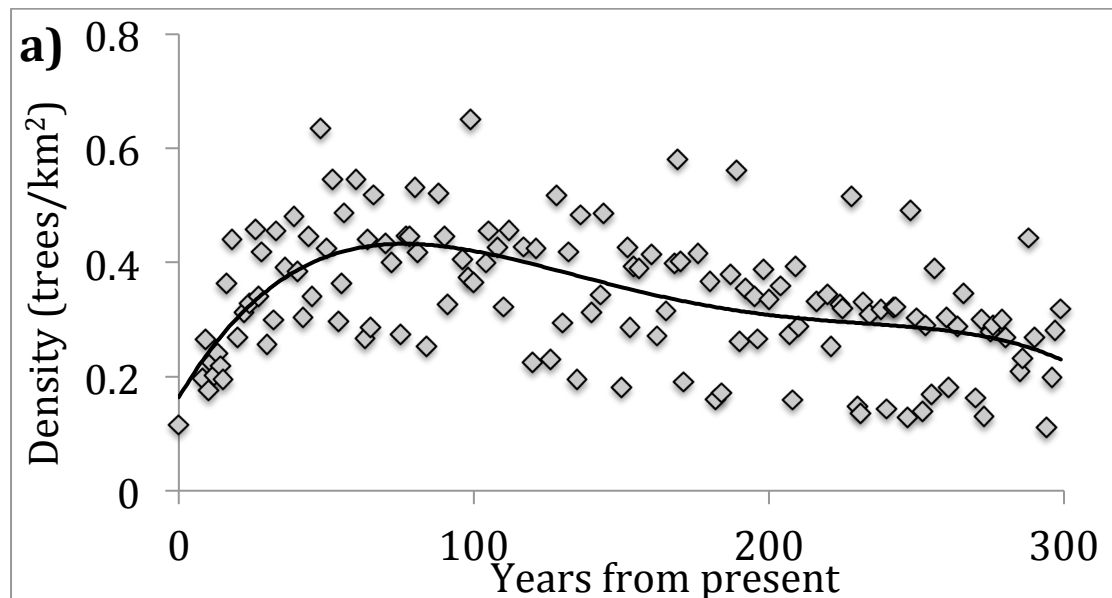
9.5 Results

We recorded a total of 1,006 isolated *Ficus* trees in our study area, of which 310 were growing on private land, and 696 were on public land (652 were growing by the roadside). Of the 202 1 km² grid squares that were adequately surveyed, 641 scattered *Ficus* trees of all species were recorded, occurring at a mean density of 3.17 ± 0.26 trees/km². When the grid squares were separated according to dominant land-use type, there was a significant difference in the mean density of *Ficus* trees between rice paddies (1.39 ± 0.13) and other land-use types (6.53 ± 0.51 ; Mann-Whitney U=836.5, Z=-9.704, $p < 0.001$).

The two most common *Ficus* species recorded in the study area were *F. religiosa* and *F. benghalensis*. We predicted similar trends in population densities for both species over time (Figure 9.3). Although the percentage change in density indicated an increase of 19.79% for *F. benghalensis* and 11.40% for *F. religiosa* over 300 years, the prediction intervals were wide for both species. The mean \pm PI of the first 10 model

intervals for *F. benghalensis* was 0.22 ± 0.43 trees/km², rising to 0.80 ± 1.56 to 0.89 ± 1.73 trees/km² for the last 10. The same figures for *F. religiosa* were 0.80 ± 1.56 to 0.89 ± 1.73 trees/km². Both species were predicted to slightly increase in density during the next 50 years, before gradual declines over the course of the rest of the model.

Our sensitivity analyses revealed that the densities of both species were most responsive to changes in annual adult mortality rates (Figure 9.4). Mortality explained approximately four-fifths of the deviance in the regression models for *F. benghalensis* and almost half of the deviance in *F. religiosa*, while also returning very large effect sizes for both species (Table 9.3). The standardised correlation coefficients indicated that a one unit increase in the mortality rate, with all other explanatory variables held at their mean values, would reduce the density of *F. benghalensis* by 0.90 trees/km² and *F. religiosa* by 0.67 trees/km². *F. benghalensis* was also sensitive to tree growth rate, which had an effect size of 0.78.



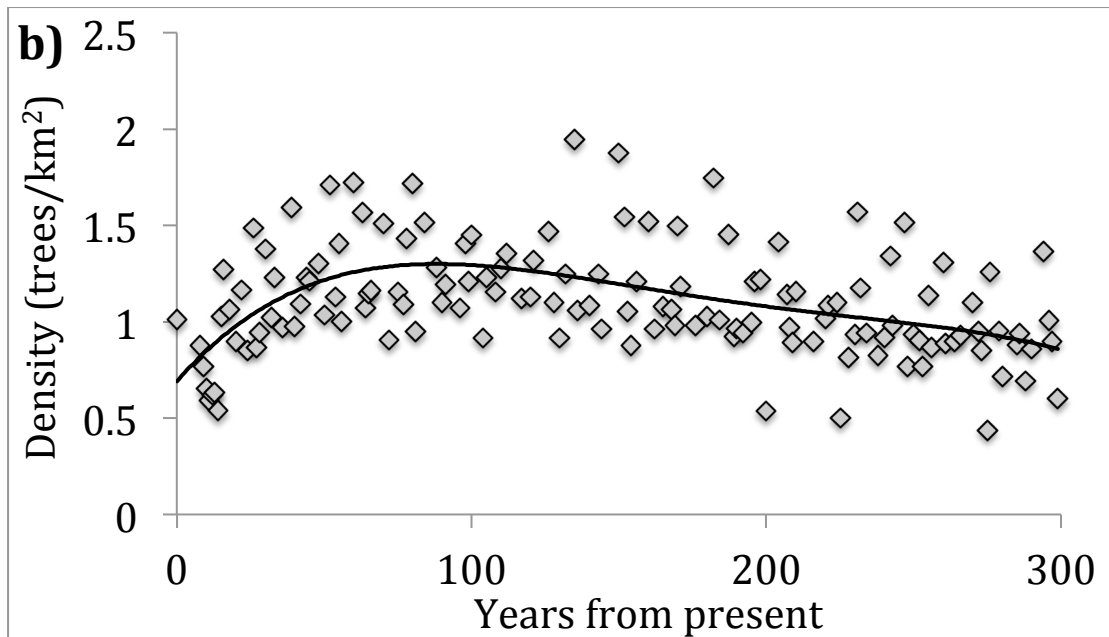


Figure 9.3: Simulation model predictions of a) *F. benghalensis* and b) *F. religiosa* population densities after 300 years under status quo conditions. Points are individual model predictions, and the black line represents the polynomial line of best fit. Note the different y-axis scales in panels a) and b).

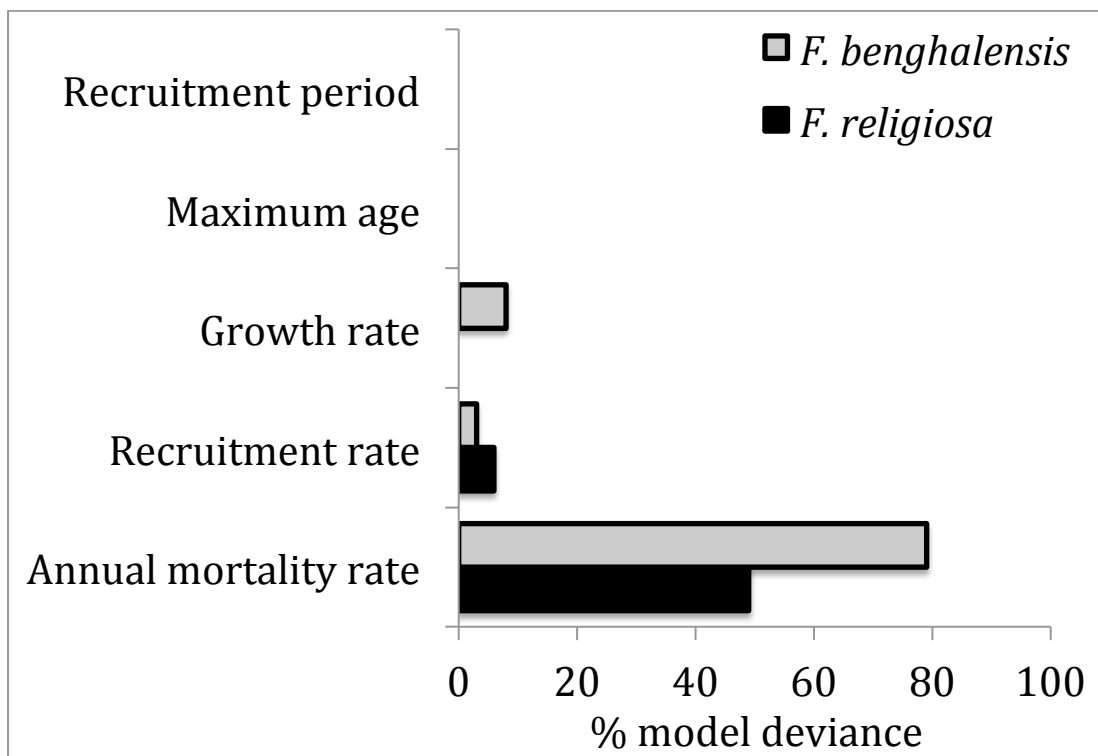


Figure 9.4: The sensitivity of the predicted density of *F. benghalensis* and *F. religiosa* in a human-modified landscape to recruitment period, maximum tree age, tree growth rate, recruitment rate, and annual mortality rate, as measured by the percentage of model deviance explained by each explanatory variable within the regression model fitted in the sensitivity analysis.

Table 9.3: Final hierarchical regression models for a) *F. benghalensis* and b) *F. religiosa*, used to determine the sensitivity of each species to the explanatory variables. Variables were entered in ascending order, and the dependent variable, the density of mature *Ficus* trees/km², was Log10(x+1) transformed prior to analysis. *p* values are inappropriate for model selection using simulated data, so the effect size was calculated using Cohen's *f*² and used to identify the most sensitive parameters in the model.

Variable	Unstandardised coefficient (B±S.E.)	Standardised coefficient	Effect size (<i>f</i> ²)
a) <i>F. benghalensis</i>			
Constant	-0.39±0.15	-	-
Annual mortality rate	-11.21±0.23	-0.90	3.79
Recruitment rate	0.07±0.01	0.18	0.17
Growth rate	-0.02±0.002	-0.28	0.78
Maximum age	0.00±0.00	0.01	0.00
Recruitment period	0.003±0.01	0.02	0.00
b) <i>F. religiosa</i>			
Constant	0.18±0.08	-	-
Annual mortality rate	-2.61±0.16	-0.67	0.95
Recruitment rate	0.02±0.003	0.24	0.13
Growth rate	0.00±0.001	-0.003	0.00
Maximum age	0.00±0.00	0.07	0.01
Recruitment period	-0.01±0.004	-0.05	0.00

Our stress test results indicated that both species are particularly vulnerable to increases in mortality, although reductions in recruitment are also likely to induce a decrease in density (Figure 9.5). In the first stress test (with lower recruitment rates), *F. benghalensis* was predicted to decrease in density to 0.04±0.07 trees/km² (mean±PI) over 300 years (82.51% lower than the status quo model). *F. religiosa* was predicted to follow a similar path, decreasing to 0.10±0.19 trees/km² in 300 years'

time (87.90% lower than the status quo model). The second stress test investigated the effect of higher mortality. For *F. benghalensis*, a more than four-fold increase in mortality, to 0.40 ± 0.10 (mean \pm SD) mature trees per year, was predicted to precipitate a fast and substantial fall in the density of this species to 0.002 ± 0.003 trees/km² (mean \pm PI) after 300 years. A similar increase in mortality, to 0.28 ± 0.07 (mean \pm SD) in *F. religiosa*, also saw the species fall in density, in this case to 0.01 ± 0.02 trees/km² (mean \pm PI) after 300 years. The final stress test investigated the effects of decreasing recruitment rates while simultaneously increasing mortality rates. Predicted densities of *F. benghalensis* dropped to less than one-thousandth of a tree/km², representing a 99.84% decrease compared to the status quo. *F. religiosa* population densities were also predicted to decrease, with a 99.61% drop to 0.003 ± 0.01 trees/km².

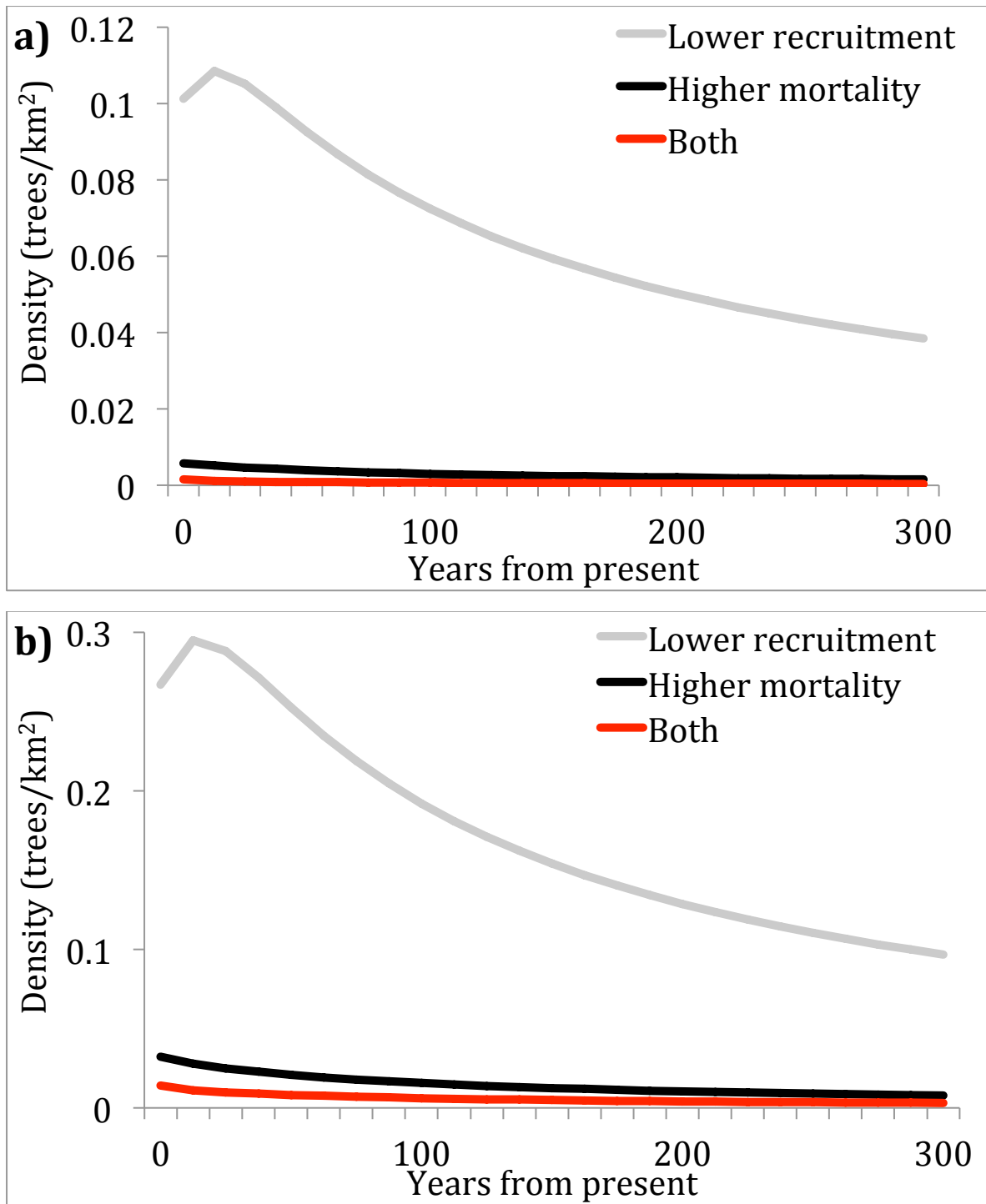


Figure 9.5: Stress test results for a) *F. benghalensis* and b) *F. religiosa*. Each line relates to a specific stress test, and shows the mean estimate of all model runs (100 in each scenario). The three stress tests were: Stress test 1) lower recruitment; Stress test 2) higher mortality; Stress test 3) both lower recruitment and higher mortality. Note that the panels have different y-axis scales.

9.6 Discussion

Our results indicate that the density of *Ficus* trees in the landscape is likely to remain stable, or perhaps slightly increase, over the next 300 years. Both *F. benghalensis* and *F. religiosa* displayed similar projected trends, with considerable mean increases over the next 100 years, before a gradual decline. Given the extent of deforestation within the life-span of a *Ficus* tree in our study area, it may be possible that the predicted increase in densities reflects the response of these species to a population bottleneck, which may result in the restoration of population densities to plausible historical levels. Indeed, the final mean densities of 0.26 trees/km² for *F. benghalensis*, or 0.89 trees/km² in the case of *F. religiosa*, are still considerably lower than the density of mature *Ficus* trees estimated in other study systems. In Bolivia, for example, Fredericksen et al. (1999) estimated that the density of particular *Ficus* species ranged from 30–170 trees/km², depending on species and habitat. In semi-dry forest habitat, the total density of all species combined reached 680 mature individuals per km².

Fredericksen et al. also found *Ficus* saplings to associate strongly with disturbed land, showing a preference for areas with moderate canopy cover (mean=66%) and recent soil disturbance (Fredericksen et al., 1999:157). As our study area is currently experiencing extensive human land-use, it seems likely that suitable micro-habitats for *Ficus* seed germination and establishment are widespread. Furthermore, the high recruitment rates used to parameterise the original model were influenced, to a considerable degree, by the high densities of immature *Ficus* individuals we recorded growing epiphytically in the crowns of shade trees in tea estates. To provide optimal growing conditions, grids of *Albizia odoratissima* are routinely planted in Assamese tea estates, providing a light canopy cover. Once these trees age, hollows form, which hemi-epiphytic *Ficus* species such as *F. religiosa* and *F. benghalensis* favour as

seedlings. However, after 70–80 years, tea plant productivity decreases, and so both tea plants and shade trees are removed before re-fertilizing the land. As many of the tea estates in our study area were planted by British colonials during the first half of the 20th century, the high abundance in hemi-epiphytic *Ficus* saplings we found would be expected. However, even during our study period, old tea estates were being cleared, which would cause a major reduction in the overall recruitment rates of *Ficus* in the landscape.

The stable or slight increase in *F. benghalensis* and *F. religiosa* densities contrasts strongly with previous studies of scattered tree regeneration. In their study of scattered trees in human-modified landscapes in Spain, the United States, Australia and Costa Rica, Gibbons et al. (2008) predicted that mature trees would be lost from all four landscapes in 90–180 years under current management regimes. Similarly, Le Roux et al. (2014) found the density of hollow-bearing trees in urban parks in Canberra, Australia, was predicted to decline by 87% over the next 300 years. Our prediction of stable or increasing *Ficus* populations provides a positive exception to declines expected in other scattered tree communities. As discussed above, this may partly be a result of *Ficus* trees regenerating successfully on degraded land. It may also be related to the human-uses of *Ficus* trees, which rarely provide commercial grade timber (Fredericksen et al., 1999; Felton et al., 2013), and which in our study area at least are offered some degree of protection due to their sacred status (Wilson & Wilson, 2013; Cottee-Jones et al., *in review*). These ecological and social properties may combine synergistically to help differentiate the future of isolated *Ficus* trees in Assam from other scattered trees, and may therefore play a key role in conserving the communities of frugivorous birds and mammals that these trees support.

Unlike other scattered trees, however, *Ficus* species are also dependent on pollinating fig wasps for reproduction and therefore population persistence (Bronstein et al., 1990; Anstett et al., 1995; Mawdsley et al., 1998). In their estimates of the minimum viable population needed for figs to persist over 1,000 years, Anstett et al. (1997) modelled fig–fig wasp mutualistic population dynamics. They found that species which flowered with some seasonality, as observed for both species in this study, a minimum population of 259 may be needed to give a pollinating fig wasp population a 99% chance of persistence over 1,000 years. In our study area, we only recorded 117 mature *F. benghalensis* trees, which suggests individuals are reproducing with trees beyond our study area (although a follow-up paternity analysis would be useful in testing this assumption; Nason et al., 1996). If figs were not capable of breeding with individuals beyond the study area, it is worth noting that the current densities of both species are already below the population threshold predicted by Anstett et al. to give a 99% chance of survival over 1,000 years (which in our study area would be 1.28 trees/km²). Although our stress tests indicate that both species would become locally extinct with substantial increases in mortality, it would be interesting to study whether population decreases in density to a mean of 0.04 trees/km² in *F. benghalensis*, or 0.10 trees/km² for *F. religiosa*, as simulated by our first stress test, would still be viable under Anstett et al.’s fig wasp population model.

A final point to consider is the identification of growth rate as an important predictor of *F. benghalensis* survival. Growth rate was not identified as an important predictor in Gibbons et al.’s (2008) study of four scattered tree populations, nor Gibbons et al.’s 2010 analysis of Australian forestry population dynamics. This result may reflect uncertainty in our tree age data, but by accounting for a wide variation in these estimates, we were still able to establish a strong association with mortality as a major

driver of demographic change. If, however, there is a biological explanation for this result, it may be related to the variety of growth forms exhibited by *Ficus* plants of the same species at different stages of their life cycle, or in different environments. Depending on the site of germination, *F. benghalensis* can grow as an epiphyte before strangling its host to become a tree, or it can grow as a free-standing tree. This variation, combined with the availability of nutrients, light, and moisture, may increase the range of growing rates, and help account for the sensitivity of this species to growth rate. If the density of *F. benghalensis* does decrease by 0.28 trees/km² for every one unit increase in growth rate, as indicated by our sensitivity analysis, higher productivity linked to a warming climate may have serious consequences for *F. benghalensis* population densities in the future (Parmesan et al., 2013; Franks et al., 2014).

9.7 Conclusion

The significance of fig trees in tropical forests is already well established. There is increasing evidence that they may also play a critical role in sustaining species assemblages and ecological function beyond the forest edge. The loss of scattered *Ficus* trees from tropical human-modified landscapes may therefore cause considerable, and perhaps cascading, decreases in species richness and seed dispersal in these areas. Our results indicate that scattered fig trees are not expected to decline in this part of rural Assam, which unlike previous studies of scattered trees, indicates that they do not represent the “living dead”. However, our sensitivity analyses and stress tests do indicate that policies and social norms, which currently serve to minimise mortality in mature trees, will be of particular importance in safeguarding *Ficus* populations, while it would also be prudent to monitor the effects of climate change on *Ficus* trees.

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CHAPTER 10:

Felling *Ficus*: the cultural standing of fig trees in a rural

Assamese community, India

10.1 Preface

While working and living in rural Assam, it soon became apparent that fig trees have a very special social status. A questionnaire based survey of local attitudes towards figs in the study area had already been conducted (Appendix 3), and so to gain a deeper understanding of the relationship between people and figs, and to understand the consequences of this relationship for the abundance and distribution of figs, this chapter adopts an ethnographic, qualitative approach to human–*Ficus* understandings in Assam.

Authors: H. Eden W. Cottee-Jones, Robert J. Whittaker

The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J. Analysed the data: HEWC-J. Wrote the paper: HEWC-J, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This chapter has been accepted with revisions by *Ethnobiology Letters*.

10.2 Abstract

Scattered *Ficus* (Moraceae) trees are critically important for the conservation of biodiversity in tropical rural landscapes. By providing large fruit crops, they help maintain seed dispersal networks and facilitate forest restoration. The conservation of *Ficus* trees scattered across rural landscapes is therefore vital for the preservation of ecosystem services and biodiversity beyond the borders of protected areas. Given the threats scattered trees face, it is increasingly important to identify locally grounded conservation strategies, which accommodate existing perceptions of *Ficus* trees, and so stand the best chance of being effective. Here we use ethnographic techniques to assess the attitudes of villagers towards *Ficus* trees in the village of Komargoan and its surrounds in Assam, India. Here, as reported in other parts of South Asia, we found *Ficus* trees held significant sacred status, which included taboos prohibiting cutting them down. However, we discovered mixed and sometimes confused understandings of the religious attributes of *Ficus* trees, which were believed to be inhabited by either gods or ancestral spirits. The main benefits people associated with *Ficus* trees were their aesthetic beauty and large size, along with the shade provided during the heat of the day. The religious, aesthetic, and practical benefits of *Ficus* trees were not sufficient, however, to prevent their felling when they incurred economic costs, although often saplings would be planted in another place as compensation. An interesting and unexpected social norm was reported with regards to the planting of *Ficus* trees, where only respected members of the community, usually older men, had the status to plant such a significant tree. Any conservation strategy aiming to sustain the abundance of *Ficus* in rural Assam is more likely to be successful if these cultural views are taken into account.

Keywords Assam, conservation strategies, cultural values, *Ficus*, sacred trees, scattered trees

10.3 Introduction

Ficus trees are considered to be critical components of forest ecosystems across the tropics (Terborgh, 1986; Lambert & Marshall, 1991; Shanahan et al., 2001). Recently, their role in conserving frugivorous communities, and in maintaining ecological function in rural landscapes, has also been identified (Guevara & Laborde, 1993; Eshiamwata et al., 2006; Barua & Tamuly, 2011; Caughlin et al., 2012; Barua et al., *in prep*; Cottee-Jones et al., *in review*). The ecological benefits they provide in rural landscapes are dependent on their persistence as networks of scattered trees (Manning et al., 2006). While many scattered tree ecosystems are declining across the globe (Gibbons et al., 2008), scattered *Ficus* trees face a peculiar set of challenges due to their close connection to religious and cultural values in some societies at least (Mawdsley et al., 1998; Sitaramam et al., 2009). For example, in Madagascar, scattered *Ficus* trees are not cut for fear of offending the ancestors they represent (Martin et al., 2009), while in India *F. religiosa* and other species play an important role in Hindu and Buddhist beliefs (Chandrakanth et al., 1990; Gadgil & Guha, 1993; Dutta, 2006; Kumar et al., 2011). While an understanding of cultural values is essential for effective conservation in human landscapes (Berkes, 2004; Jones et al., 2008; Chazdon et al., 2009; Sherren et al., 2010; Harvey et al., 2011), a deeper understanding of the local attitudes towards scattered *Ficus* trees in particular may be needed to ensure their conservation.

With these concerns in mind, our research questions were: 1) what religious attributes do people endow upon *Ficus* trees? 2) What are the local attitudes towards *Ficus* trees? 3) What strategies may be successful in boosting *Ficus* recruitment rates? 4) How should conservationists adapt their strategies to account for local beliefs and norms relating to *Ficus* trees?

10.4 Methods

The study was conducted between October 2012 and June 2013 in the Golaghat District of Assam, North-eastern India. Fieldwork centred on the village of Komargoan at (N26 38.221 E93 45.377), but included work in a wider area bounded by the Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93 54.978. The original habitat of moist subtropical deciduous forest was largely cleared following the local commercialisation of tea production in 1840 (Shrivastava & Heinen, 2007). The landscape is an agricultural mosaic, with a heterogeneous assortment of smallholder rice cultivation, tea estates, and village home gardens. Most of the population are rice farmers with supplementary cash and subsistence crops (Barua et al., *in press*). The area has a population density of 302 people/km² (GOI, 2011).

To gain a deeper understanding of social relations between local people and scattered *Ficus* trees in the study area, detailed observation and open-ended interviews were conducted (Hammersley & Atkinson, 2007). Ethnographic observations centred on the experience of living within an Ahom community in the village of Komargoan. The Ahom are the dominant social group in Assam, who are Hindu and primarily speak Assamese. In Komargoan the first author resided with a rice farming family in a recently constructed brick house with a temporary tin roof. Their wealth was typical of the households in the area. They earned money from farming a moderate area of rice paddies, and otherwise produced milk, eggs, and fruit in their home garden for subsistence. During this time, the primary researcher cooked, cleaned, and helped with tasks around the house, as well as eating and socialising with the household and neighbours in the villages. This “deep hanging-out” (Geertz, 1998:69) allowed the primary researcher to build up a rapport with the community, and to uncover the suppressed perspectives towards *Ficus* trees, that were hard to garner from conversations

with informants who were more overtly aware of the researcher's position as a foreign scientist (Mackenzie, 1994).

Over the course of the study period, discussions were held between the first author and members of the community in Assamese, English, and in Assamese through a translator (who was a native Assamese and fluent English speaker). In cases where a translator was needed, the translator had been trained in the importance of providing an accurate and detailed account of the exchange, and discussions of how questions should be framed were held both before and after meetings where translation was necessary (Maranhão, 2003). Although the use of a translator increased the formality of some discussions, most of these interactions were informal and conversational, which enabled the first author to ask questions in a naturalistic manner.

To augment the information gathered during casual exchanges, we also conducted a series of 12 interviews with key informants who may have been able to offer some additional in-depth insights (Hammersley & Atkinson, 2007). These interviews were still informal, and interviewees were asked open-ended, unstructured questions. Interviews lasted between 40 minutes to one hour and were transcribed by hand. As men are traditionally considered to be the head of the household in Komargoan, nine of the interviewees were male, while the remaining three were female, and interviewee ages ranged from 29–80 years. Interviewees included women who lived next to *Ficus* trees, village elders, priests, and tea estate managers. We asked each individual a series of standard questions prepared in advance, along with others that arose during the course of the interview (Martin, 1995; Platt et al., 2012). The topics covered in each interview included: 1) the religious significance of *Ficus* trees; 2) the benefits provided by *Ficus* trees; 3) the problems associated with *Ficus* trees; 4) whether *Ficus* trees were cut down in the area; and 5) how people could be encouraged to plant more *Ficus* trees. After being granted consent, two interviews were recorded on camera,

and all were transcribed by hand during the interview. Interviewees were given false names to preserve their anonymity.

We adopted an inductive thematic approach to data analysis, in which meanings and key issues emerged from the data through the careful analysis of all records. Several sources of data were used to generate a more comprehensive understanding of the emerging themes, including observations, conversations, and interviews.

10.5 Religious status of *Ficus* in Assam

There was widespread acknowledgement amongst the inhabitants of Komargoan and neighbouring villages that *Ficus* trees are sacred, supporting previous reports from the Indian Subcontinent (Chandrakanth et al., 1990; Gadgil & Guha, 1993; Ingles, 1995; Dutta, 2006; Sitaramam et al., 2009; Kumar et al., 2011). Temples were common features at the base of both large “*jorigos*” (*F. religiosa*) and “*borgos*” (*F. benghalensis*), with another study conducted in the same locality recording temples or shrines at the base of 14.65% of all mature *Ficus* trees (Barua et al., *in prep*). These include large modern temples, constructed with the proceeds of community fundraising efforts, to small shrines, consisting of a red banner as a gift to the gods, or even a poster depicting a god. Historically, *Ficus* trees have been described as important sites of worship since the Buddha gained enlightenment meditating under a large *F. religiosa* (Spiro, 1982; Chandrakanth et al., 1990; Lewington & Parker, 1999). Even trees without shrines are said to be sacred, however, with Mimpì, a local villager, reporting that people prayed at all *Ficus* trees, including a *borgos* growing by her house, which had no shrine.



Figure 10.1: A *F. religiosa* with an orange ribbon around its trunk to signify its sacred attributes. This picture was taken in the village of Komargoan, Assam, by HEWC-J.

Several villagers reported that gods lived in the *Ficus* trees themselves (Figures 10.1 & 10.2). Priest Purshat, who was responsible for a temple at a large *borgos*, explained that evidence for gods inhabiting *Ficus* trees could be found in the pure white waxy sap they produce when cut, which is the blood of gods. There was some disagreement over which gods in particular inhabited *Ficus* trees. Priest Purshat described the God Dangoria, who inhabited the *borgos* next to his temple and who is a general god found all over Assam, as the only god to inhabit that tree. Other villagers claimed multiple gods inhabited *Ficus* trees, while Tika, a Nepali immigrant, argued that only Durgha, the God of power, inhabited *Ficus* trees. There was also some debate over which *Ficus* trees held sacred value, with many reporting *jorigos* to be the most important species, despite Priest Purshat arguing that *borgos* is the main god tree. A more widespread view, held by almost every interviewee, was that ancestors inhabited *Ficus* trees. The link to ancestral spirits is one that is shared by sacred groves across India

(Malhotra et al., 2001; Bhagwat & Rutte, 2006), while a very similar belief is held in Madagascan *Betsileo* communities, who view *F. tiliifolia* as a highly respected “ancestor tree”, which forms the symbolic centre of their ancestral belief system (Martin et al., 2009). Elsewhere in Africa, figs are also the focal points of local faiths that use them as sites of worship (Wilson & Wilson, 2013). In Kenya, *F. thonningii* is the medium through which the prayers of the A-Kikuyu people ascend to their God (Beech, 1913), and in Burundi and Rwanda, figs are places to worship ancestral spirits (Niyonkuru, 1995).



Figure 10.2: A temple priest in front of a *F. benghalensis* that is inhabited by the gods. A neighbouring temple was build with the proceeds of a community fundraising effort in 2004. This picture was taken just south of the village of Komargoan, in Assam, by HEWC-J.

There was some evidence that the importance of *Ficus* trees, in terms of their sacred value, was tied to their age. Hondihiram, a man who lived next to a small *Ficus* tree, commented that ancestors did not live in this particular tree, as it was too young. The link between size and age, and the relationship between large old trees and sacred value may also help explain

why slightly smaller species, such as *Demoru* (*F. assamica*) and even *Ahat gos* (*F. benjamina*) were not reported to have religious or spiritual significance (despite their appearance in Hindu sacred texts). Furthermore, while temples and shrines were common at the base of *Ficus* trees throughout the region, they were conspicuously absent from young, small trees. A trend for increased reverence of older and therefore larger trees, as opposed to smaller trees, finds some support in other cultures (Chandrakanth & Romm, 1991). In Ntumu societies in southern Cameroon, for example, particular value is attributed to age, with elders believed to be sacred through their close contact with the ancestors. This respect for elders is also transferred to large old trees, which Ntumu farmers selectively leave standing when clearing forest for fields (Carrière, 2002).

Beliefs surrounding *Ficus* trees are also being assimilated into contemporary culture in Assam, with drivers beeping their horns as they pass *Ficus* trees, and inter-city buses stopping at *Ficus* temples so the ticket collectors can quickly get off and pray for the safety of the bus. Other modern views influencing attitudes towards *Ficus* reflect wider changes in society, with Dulal, an English-speaking 42-year-old artist, arguing that people no longer really believed that gods inhabited *jorigos*, describing it as an “ancient belief”.

10.6 Benefits and uses of *Ficus*

A drop in the belief that gods inhabit *Ficus* trees, due to atheism in Dulal’s case, may result in wider changes in the abundance and distribution of *Ficus* trees in the human landscape. Here it is important to understand the way people use and benefit from *Ficus* trees, to judge how important their local sacredness is to their perpetuation. Amongst the uses of *Ficus* trees, at least one major use was tied to religious beliefs. On holy days, it was common to see people reach or climb up a *jorigos* and cut a small branch with young leaves off. This branch was then used in “*puja*” or worship, and is important in many religious ceremonies in Assam. The most commonly cited benefit of scattered *Ficus* trees was the shade they provided,

giving “cool air” and “a large shadow” for people and livestock to shelter under during the heat of the day, when the temperature could exceed 35°C. This heat helps explain the occurrence of *Ficus* in open agricultural areas, such as paddy fields, and their abundance in public places, such as bus stops and junctions. Indeed, in another study in the same region, 64.81% of 1,006 mature *Ficus* trees were growing within 10 m of a road (Cottee-Jones et al., *in review*). Another frequently cited benefit, which complements their shade giving properties, was their ability to decrease wind speeds using their “big branches”. On a slightly less practical level, villagers very commonly reported a major benefit of *Ficus* trees to be their beauty. Examples of beautiful *Ficus* trees tended to be old and very large individuals, usually with complex trunk patterns and aerial roots. The aesthetic beauty of these trees recalled other large charismatic trees, such as European oaks (*Quercus* spp.) or Australian eucalypts (*Eucalyptus* spp.), and many of the religious beliefs surrounding these *Ficus* trees may have derived from common sentiments of inspiration or awe associated with large trees around the globe (Lewington & Parker, 1999). Indeed the literal translation of *borgos*, the Assamese name for *F. benghalensis*, is actually “big tree”.

While many sources list the medicinal properties of *Ficus* trees (Dutta, 2006; Lansky et al., 2008; Kumar et al., 2011), villagers we met did not seem aware of any illnesses that *Ficus* products could help prevent or cure. Furthermore, although the fruit of *F. carica* is very popular in the Middle East and elsewhere (with over 1 million tons of dried figs produced annually) the locals in Assam did not report eating *Ficus* fruit (FAO, 2013). However, livestock were reported and frequently observed to eat fallen *Ficus* fruit, although the collection of *Ficus* leaves for livestock fodder was not common, unlike in nearby Nepal where some estimates suggest fig leaves provide 40–50% of animal feed (Pandey, 1982; Kunwar & Bussmann, 2006). *Ficus* wood was not used as a building material, for construction or furniture, as the wood was said to be of very poor quality. Villagers also said

it burnt very poorly when used as firewood, and was not worth cutting down for that purpose. Although quite close geographically, we received no reports of *Ficus* sap being used to make sticky bird glue traps, as Chin hunters do in Western Myanmar (Platt et al., 2012). In East Africa and Madagascar, scattered *Ficus* trees have been used to demarcate land boundaries or sites of significance (Kakudidi, 2004; Martin et al., 2009). When we consulted villagers in Assam, they said *Ficus* trees were not used for such a purpose.

10.7 Costs of *Ficus*

Despite their sacred position in Assamese culture, the disadvantages and costs of *Ficus* trees were fairly extensive. Their large canopies, which were favoured in public spaces such as road junctions and markets, were undesired on private land, where they would very effectively shade out crops and thereby reduce agricultural productivity. Rajan, a manager at a 252 ha tea estate, commented that along with the extensive shade they produce, *Ficus* trees are also breeding areas for insect pests that can further reduce productivity. Their extensive and shallow root systems were a problem for agriculture, creating a barrier to ploughs and competing with crops for moisture and nutrients. The quantity of water *Ficus* drew-up was the focus of a complaint by the 70-year-old Konkeswar, who commented that you could not place a pump well under or near a *borgos*, as it will provide too much competition for water. This is a critical issue, as every house within reach of a groundwater source in Komargoan and the neighbouring villages received the total household water supply from a pump well. In many cases, *Ficus* trees were framed as “problem species”.

10.8 Felling *Ficus*

Given the strong economic complaints made by locals about *Ficus* trees, it was interesting to hear their attitudes and stories about cutting *Ficus* trees down. In common with Madagascan *Betsileo* society, where *Ficus* trees are not cut despite the absence of an official prohibition

(Martin et al., 2009), Komargoan villagers resist felling *Ficus*. When asked if people in her village cut *Ficus* trees down, Mimpri emphatically said that they wouldn't. This was a common response, with many worried about offending ancestors or angering gods. Indeed Priest Purshat went as far as to say that people who cut *Ficus* trees down may be punished by the gods, and may even be killed. The perceived power of the gods was illustrated by the story of Chandrajit, a mother whose house neighbours a large *borgos*. She described a dream where the gods who inhabited the *borgos* were angry, as they did not like her boundary fence being so close to their tree, so the next day her husband moved the fence back by six metres.

Similar fears also influenced Shana's decision-making. Her family live under an enormous *borgos* on a small hill, and she complained that during stormy nights they could not sleep as they were so worried the tree would break and fall on them. Their fears were fairly well founded, as weak-wooded *Ficus* trees seem particularly vulnerable to the violent monsoon storms that affect Assam for several months each year. However, she said they were too scared to cut the tree down because ancestors live in it.

Some had a more practical outlook, including Gunin, who said that if you need to cut a *Ficus* tree down, you should first plant another one for the ancestors, and Dyoti, who said you have to pray at a *Ficus* tree before you cut it down, and explain to the ancestors why it has to be felled. Reasons given for cutting *Ficus* trees involved: preventing the trees encroaching on roads, stopping them getting tangled in power lines, and because they were providing too much shade on small village gardens. Even a conservationist, Jintu, cut a mature *Ficus* tree down to improve productivity in his home garden.

An additional insight into the religious tensions over felling *Ficus* was provided by Rajan in front of a recently cleared tea plantation. After roughly 80 years tea plants become less productive, so they are removed and replaced with a nitrogen fixing plant for two years, before new tea plants and shade trees are planted. Before clearance, Rajan's plantation had a

fairly dense cover of shade trees, including two *Ficus* trees. After clearance, all the tea plants and shade trees had been removed by a bulldozer, except for the two *Ficus* trees, which now stood completely exposed in a barren expanse (Figure 10.3). Rajan revealed that the bulldozer driver had refused to knock the *Ficus* trees down because they were sacred. When asked whether he would have to leave them, Rajan said that he was waiting to find someone who did not share the same beliefs about the sacredness of *Ficus*, probably a Muslim, and would employ them to cut the trees down with a saw. The wood, he said, would be used to make fence posts. While some people, such as the bulldozer driver, refuse to compromise their beliefs, in other cases the practical problems posed by *Ficus* trees, especially on private land, induce even local conservationists to overlook their religious views and fell *Ficus*. This heterogeneity in the application of local values, especially considering the propensity of economic imperatives to triumph, suggests that aligning conservation arguments with such beliefs may lead to inconsistent results at best. While seeking to entrench these values may help reduce premature *Ficus* mortality in the short term, adopting an approach that is reconcilable with powerful economic incentives may be more promising in the long run.



Figure 10.3: A *F. curtipes* that was not felled while the surrounding tea estate was cleared of all vegetation. It was scheduled to be felled by someone who does not believe gods inhabit it. The picture was taken in May 2013 just east of the village of Komargoan, Assam, by HEWC-J.

10.9 Planting *Ficus*

The situation with regards to planting *Ficus* is also fairly complex. There was widespread support for *Ficus* planting, and many examples where people were able to share their *Ficus* planting experiences. *Ficus* were either planted as seeds or cuttings from mature trees, and were planted for a variety of reasons. Probin planted a *Ficus* by the road outside his house as it would look beautiful when it was older, Suno planted a *jorigos* in front of his shop to prevent cars crashing into it, as had happened to the neighbouring shop, Hondihiram planted a *jorigos* at a t-junction near his house to provide shade, and Gunin planted a *Ficus* tree on the banks of a stream to prevent erosion. However, all of the people above fall into a similar demographic, they are all fairly elderly men (age range 55–78). They, along with many others in the community, insisted that only senior men (about 55+) had the respect and authority to

plant a *Ficus* tree. Planting a *Ficus* tree is not a trivial act, due to its connections with the gods and ancestors, and in the study area women and young men are not considered to have sufficient societal status to plant a *Ficus*.

Attitudes may be changing, however. Dulal, who is not religious, but whose father planted a *jorigos*, argued that anyone could plant a *Ficus* tree. Bumon, a 32-year-old teacher, said that young people should be encouraged to plant all trees, including *Ficus*, while Dhekial, a 27-year-old rice farmer, would be happy to plant *Ficus* trees if seedlings were provided. In fact, several villagers were keen on the idea of restoring forests, and said they would contribute the materials needed to make a small fence (one bamboo pole, roughly 50–60 rupees, equivalent to US\$0.80–1) around *Ficus* saplings that were provided by a donor. While this is promising, the wider societal changes that are shaping attitudes about who should plant *Ficus* trees make aligning a conservation strategy with either camp potentially dangerous, with the position likely to be criticised whatever the framing.

10.10 Conclusion

Here, a deeper understanding of local customs can help inform conservation policymakers on strategies that would be sensitive to the priorities and beliefs of the local population. Taking these beliefs into account is not only the responsible ethical approach, but also increases the chance of the conservation strategy achieving success (Adams et al., 2004). In the case of scattered *Ficus* trees around Komargoan village in Assam, large species of *Ficus* held widespread sacred significance. The relationship with size is an interesting one, as small species of *Ficus*, and younger individuals of the larger species, were not reported to be inhabited by gods or spirits. Furthermore, many of the secular values of *Ficus* trees were also linked to their size: beauty, a sense of awe, and the provision of shade. And it tended to be these more practical considerations that had the largest influence over tree cutting and planting: trees that provided too much shade over villagers home gardens were removed,

while trees were planted in hot open areas to lower temperatures. Therefore we suggest that conservation strategies should recognise the spiritual significance of scattered *Ficus* trees, but not rely on this alone to safeguard their survival.

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CHAPTER 11:

Global plasticity in cultural values associated with figs

11.1 Preface

The observations in Chapter 10 provided interesting insights into the status of *Ficus* trees in Assam, and indicated promising areas that may be pursued to conserve isolated *Ficus* trees. However, little empirical work had been conducted into how these values associated with *Ficus* trees might change over space. In an attempt to discover any patterns in the values different communities hold for *Ficus* trees on a broader scale, Chapter 11 presents the results of a global survey of *Ficus* experts, and their reports of *Ficus* social values from study areas around the world.

Authors: H. Eden W. Cottee-Jones, Thomas J. Matthews, Robert J. Whittaker, members of the *Ficus* social values working group (FWG)

The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J, FWG. Analysed the data: HEWC-J. Wrote the paper: HEWC-J, TJM, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4 (excluding the numerous members of the FWG whose contributions were restricted to the completion of an online questionnaire).

This chapter is currently receiving comments from the many FWG co-authors, after which it will be submitted to Biodiversity & Conservation.

11.2 Abstract

Fig trees (*Ficus*, Moraceae) are critically important ecological components around the world's tropics and subtropics. They are also reported to hold sacred value for several social groups in Africa and Asia. However, little is known of their conservation status, locally or globally, or the true extent of these sacred properties. Here we sought to scope the conservation status of *Ficus* trees, and assess the human-uses they are valued for, at a global scale. We conducted an online expert opinion survey of 144 *Ficus* and ethnobotanical experts in nine regions around the world. We found that figs were regarded as fairly resilient to deforestation and targeted tree removal, and were not particularly vulnerable to mortality compared to other trees. The values people attribute to figs varied markedly across space, with concentrations of religious value in East Africa, South Asia, East Asia, and South-east Asia. However, there was considerable overlap between areas with high religious value and the frequency of felling *Ficus* trees. Furthermore, numerous economic concerns were provided as reasons for clearing or not planting *Ficus* trees. Therefore, when recommending conservation strategies, we suggest focusing on other important *Ficus* values, such as their aesthetic beauty, ecological role in the landscape, and ability to provide shade in non-production settings. These cultural values were widely recognised, and offer a less controversial approach to safeguarding *Ficus* populations on a global scale than a strategy focused on sacred properties.

Keywords biodiversity conservation, ethnobotany, expert opinion survey, factor analysis, *Ficus*, fig conservation, religion, social values, tropical landscapes

11.3 Introduction

Ficus L. (Moraceae), commonly known as figs, are a widespread plant genus, with approximately 750 species found across the world's tropics and subtropics (Berg, 1989; Berg & Corner, 2005). The unique mutualistic relationship between *Ficus* and their fig wasp pollinators ensures they produce fruit throughout the year, which, in combination with their extremely large crop sizes, makes them a critical resource for many insects, birds, and mammals in tropical forest ecosystems (Terborgh, 1986; Shanahan et al., 2001; Chaudhary et al., 2012). There is also growing evidence that figs play an important ecological role beyond the boundaries of forest ecosystems, in human-modified landscapes. Here they conserve avian frugivore populations, maintaining seed dispersal functions, and enable forest restoration (Barua et al., *in prep*; Cottee-Jones et al., *in review*).

Aside from their important ecological roles in forest and non-forest ecosystems, figs are also believed to have important religious properties (Caughlin et al., 2012). *Ficus religiosa*, for example, is a holy tree in both Hindu and Buddhist faiths (Dutta, 2006). In Buddhist tradition, the Buddha received enlightenment by meditating under a *F. religiosa*, while in Hindu tradition, *F. religiosa*, along with four other species of *Ficus*, form the *Panchallava*, whose leaves are used for religious ceremonies and other important rites (Dutta, 2006; Kunwar & Bussmann, 2006). *Ficus* trees also hold sacred value in Madagascar, where the *Betsileo* community regard them as ancestor trees, inhabited by spirits and protected by social regulations (Martin et al., 2009). These sacred values may position *Ficus* trees as micro-scale sacred sites, which like sacred groves, can be conserved by upholding traditional belief systems (Bhagwat & Rutte, 2006).

Beyond Asia and parts of East Africa, figs have not been reported to hold sacred value (Caughlin et al., 2012). However, a range of other economic uses have been attributed to

Ficus (Shi et al., 2014). In Costa Rica, cattle farmers value *Ficus* trees for their use as fence posts, firewood, and live fences (Harvey & Haber, 1999), in Myanmar *Chin* hunters use their sap to make traditional bird-catching glue (Platt et al., 2012), while in India they are used in traditional medicine to treat numerous ailments, ranging from jaundice to ulcers (Kumar et al., 2011).

Despite their reported ecological, cultural, and economic benefits (Wilson & Wilson, 2013), *Ficus* trees are often overlooked in conservation strategies (for example: SAN, 2010; RSPO, 2013). Developing a fuller understanding of the economic and cultural values of *Ficus* trees, and how they vary across space, can help inform conservation strategies. A well-informed approach that is consistent with local values and beliefs would not only improve the ethical basis for a conservation measure, but would also improve its effectiveness (Berkes, 2004). Information on the range of values associated with *Ficus* may help place them in an appropriate conservation framework, which could drive their conservation through an ecosystem services, sacred site, or agricultural sustainability approach (Bhagwat & Rutte, 2006; Naidoo et al., 2006).

Here we seek to understand the contrasting strength of economic and cultural values associated with *Ficus* trees, and how they vary geographically. In particular, we aim to 1) identify any trends in the conservation status of *Ficus* trees; 2) examine how values associated with *Ficus* trees change over space; and 3) determine measures which may be successful in *Ficus* conservation.

11.4 Methods

11.4.1 Expert survey

To obtain data on a global scale, we conducted an online expert survey to quantify human–*Ficus* values. Synthesising the opinions of experts through expert elicitation is a technique that has been recognised for several decades in social science and risk assessment (O’Hagan et al., 2006; Donlan et al., 2010). In data-poor scenarios, expert elicitation is becoming increasingly useful in guiding decision-making in the conservation sector (Martin et al., 2005; Donlan et al., 2010; Sutherland et al., 2011; Laurance et al., 2013). We sought to apply these techniques to questions concerning the human–*Ficus* relationship by surveying *Ficus* experts around the world.

To conduct this survey, we first selected nine countries or regions (herein collectively referred to as regions) that spanned the American, African, and Asia-Pacific tropics and subtropics that we were interested in investigating. They were: India, China, The Philippines, South-east Asia (Indonesia, Malaysia, Brunei), Papua New Guinea, East Africa (Uganda, Tanzania, Kenya, Ethiopia), Madagascar, Central America (Mexico, Panama, Costa Rica), and the Amazon (Brazil, Bolivia, Peru). For each region, we aimed to gather a minimum of 10 completed questionnaires as a threshold for inclusion in the analysis. We achieved this in all cases except for Madagascar, where we obtained six completed questionnaires. Before retaining Madagascar in the study, we conducted a saturation test to determine how much new information was provided by each additional questionnaire (Lung et al., 2012; Laurance et al., 2013). The result of this test indicated that it was appropriate to retain Madagascar in the study (see Supporting information A, Section 11.10).

Experts who had conducted research at a field site with *Ficus* trees, and who were familiar with the local uses of these trees, were invited to participate in the study. These experts were identified by searching the literature, and through discussions with “gatekeepers” of *Ficus*, tropical ecology, and ethnobotany interest groups. To search the literature, we used combinations of keywords including *Ficus*, ethnobotany, ethnopharmacy, ecology, and country names in Google Scholar. We searched all records first, and then limited our search to work published after 2010 to increase the likelihood of identifying an expert with a recent interest in the topic and a working email address. To avoid selecting clusters of like-minded experts, we only invited one author from each peer-reviewed paper to participate in the survey. Each expert was invited to participate in the study by a customised email. In return for completing a questionnaire, experts were offered the option of inclusion as a co-author in any publication using their input.

11.4.2 Questionnaire design

We prepared a questionnaire with 36 short-answer questions, which covered topics on the economic, environmental, and cultural attitudes towards *Ficus* trees (see Supporting information B, Section 11.10). The questions were multiple-response, and each respondent was asked to select an answer on a three-, four-, or five-point scale, depending on the section. In addition, each question had an “unsure” option to avoid diluting high-confidence, accurate responses with low-confidence, guessed responses (O’Hagan et al., 2006; Laurance et al., 2013). In a further attempt to reduce the chance of low-confidence responses affecting the accuracy of the results, respondents were asked to evaluate the accuracy of their responses by rating their confidence in the answers provided. Responses with a low-confidence rating were excluded pair-wise from analysis. At the start of the questionnaire, each respondent was asked to name a particular study area they had worked in, and confine their answers to that area. Respondents were given the option of

anonymity, which 9.72% elected to accept.

11.4.3 Statistical analyses

Questionnaire responses were coded and then tested for normality. In cases where the assumptions of parametric tests were met, differences in outcome variables were tested with one-way Analysis of Variance tests (ANOVA), combined with follow-up post hoc tests where necessary. In situations where the coded data did not conform to a normal distribution, non-parametric chi-squared, Kruskal-Wallis, and Mann-Whitney U tests were performed (Field, 2009).

To identify trends in *Ficus* tree abundance, experts were asked to estimate how the abundance of *Ficus* trees in their study area had changed while they had worked there. Experts who provided answers with a high degree of certainty, and who had worked in their study areas for a period spanning at least 10 years, were retained for analysis. Responses were coded “2” for an increase of 25–50%, “1” for an increase of 5–25%, “0” for no major change, “-1” for a decrease of 5–25%, and “-2” for a decrease of 25–50%. The mean scores for each region were then analysed for the existence of significant differences using a Kruskal-Wallis test.

To discover whether changes in fig abundance are more or less dramatic than changes in the abundance of other trees, experts were asked whether figs were declining faster, at about the same rate, or slower, than other trees. After removing uncertain answers, these responses were coded -1, 0, or 1, respectively. We then used a chi-squared test to examine whether the differences reported were statistically significant.

We identified reasons for *Ficus* declines by asking experts how frequently *Ficus* trees were cut down in their study area. After uncertain answers were excluded, responses were coded: never=1, rarely=2, occasionally=3, and frequently=4. We used an ANOVA to

identify any significant differences across the nine regions. Experts were asked to provide the main reasons people had for cutting *Ficus* trees down. These reasons were classified into emergent groups, and a chi-squared test was used to determine whether some reasons were cited more frequently than others due to chance alone.

We asked 13 questions covering the values local people in each expert's study area held towards or derived from *Ficus* trees. To uncover any underlying trends in responses to this section, we conducted a factor analysis to reduce the dimensions to a manageable number for further evaluation. We scored all responses to questions in this section 1–4, and excluded missing values pair-wise. We performed a Principal Components Analysis (PCA) with the responses to the 13 questions, using varimax orthogonal rotation with a Kaiser stopping criterion of eigenvalues greater than 1. We used the Kaiser-Meyer-Olkin (KMO) measure and Bartlett's test of sphericity to assess the adequacy of our sample size and data correlations, followed by a reliability analysis using Cronbach's α to test the suitability of our survey questions. The factors produced by the PCA were compared on a region-by-region basis using an ANOVA with Hochberg's GT2 post hoc tests. We also used a Levene's test for homoscedasticity, followed by a Welch test with Games-Howell post hoc tests in cases where the assumption of equal variances was not met.

We investigated the relative economic, environmental, and cultural importance of *Ficus* trees compared to other trees in different regions by asking respondents to rate their importance on a five-point scale (much less=-2, slightly less=-1, no difference=0, slightly more=1, much more=2). After removing uncertain answers, the global averages for each category were calculated and compared using a chi-squared test. Mean scores for each region were also calculated in each category. The frequency of regions obtaining a mean score in 0.25 cohorts between -2 and 2 were plotted for economic, environmental, and cultural value, where positive scores indicated *Ficus* trees had higher value in a particular

category than other trees, and negative scores indicated *Ficus* trees had lower value than other trees.

We assessed potential measures to increase *Ficus* recruitment by asking experts whether figs were planted in their study area (responses were coded: never=1, rarely=2, occasionally=3, and frequently=4). Mean scores for each region were calculated and tested for significant differences using a Kruskal-Wallis test, with follow-up Mann-Whitney U tests and a Bonferroni correction to examine differences between particular regions of interest. The reasons provided by experts for planting *Ficus* trees were grouped and counted, and tested for significance using a chi-squared test. We also asked experts to predict the likelihood of two particular incentives succeeding in encouraging *Ficus* planting in their study area: providing free *Ficus* seedlings, and providing free fencing around *Ficus* seedlings. Answers were coded 1=would not be successful, 0=may be successful, 1=would be successful. After uncertain answers were discarded, the group sizes were compared using a chi-squared test. All analyses were conducted in SPSS 22.0 (IBM, 2013).

11.5 Results

A total of 144 experts responded to the survey, providing perspectives from 27 countries. The majority of the respondents were from the academic sector (78.74%), with other respondents working in the non-profit (13.39%), tourism (9.45%), consulting (4.72%), and government (4.72%) sectors. The experts averaged 14 years and six months of experience in their field sites (SD=14 years). The most common land-use types in their study areas were mixed agriculture (35.46%), secondary forest (14.18%), and plantations (11.35%).

In assessing the conservation state of *Ficus* trees, 46 respondents had worked in their study area for over 10 years, and provided estimates of *Ficus* abundance changes with a high degree of confidence. On average, respondents in six of the nine regions reported a decrease in *Ficus* abundance, the largest of which was reported in East Asia (Figure 11.1). However, a Kruskal-Wallis test found that there were no significant differences between regions ($H_{(8)}=10.65, p=0.22$).

Of the 102 respondents who provided an estimate of the change in abundance of fig trees relative to other trees with a high degree of certainty, 51.96% reported that fig trees were declining at about the same rate, 42.18% reported that figs were declining slower than other trees, and just 6.86% reported that figs were declining faster. These differences were significant ($\chi^2_{(2)}=31.49, p<0.001$). Of the seven respondents who said figs were declining faster than other trees, two were from each of South Asia and East Africa, with single reports coming from Central America, South-east Asia, and the Philippines.

The regions with the highest mean scores in response to the question “Are fig trees cut down in your study area?” were Papua New Guinea, East Asia, and South Asia (Figure 11.2). However, the differences between regions were not significant ($F_{(8,116)}=0.68, p=0.71, r=0.05$). The main reasons given for cutting figs down were: as part of general land clearance (38.43%), to minimise shade in agricultural areas (11.11%), and for use as timber (11.11%; Table 11.1). The difference between the frequency of citations for particular reasons was significant ($\chi^2_{(12)}=340.95, p<0.001$).

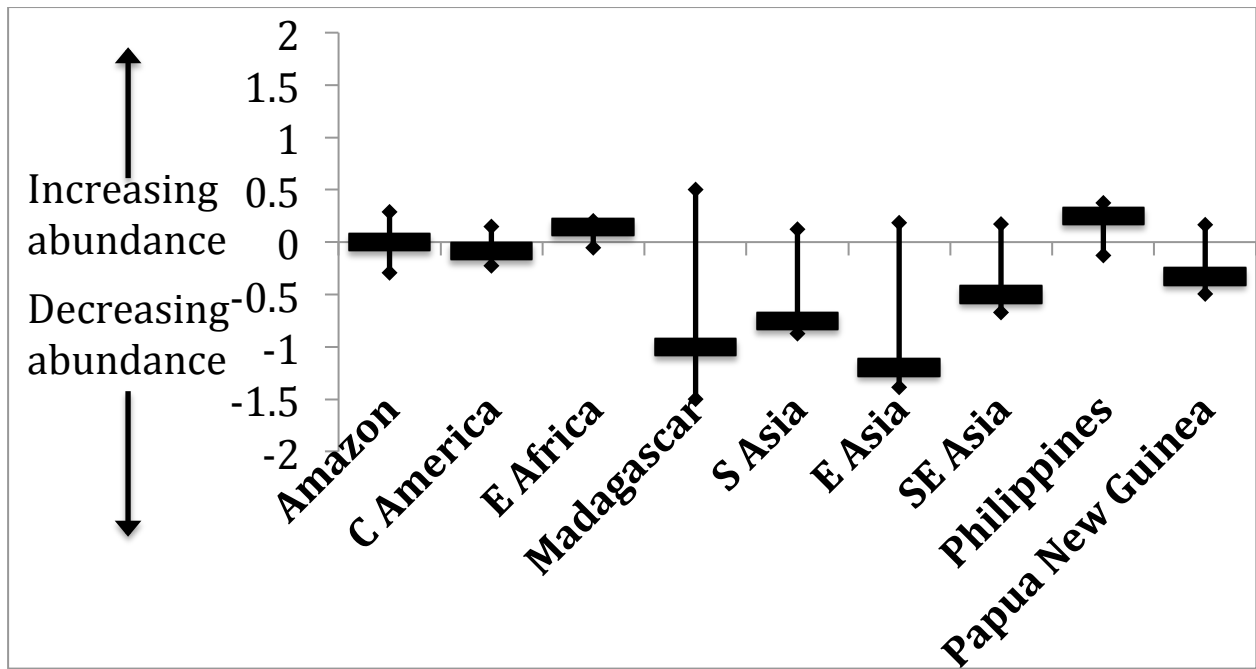


Figure 11.1: Reported changes in *Ficus* abundance in nine regions. Thick horizontal bars are mean scores for each region, thin vertical bars represent 1 SD. Experts were asked to specify a study area they had worked in, specify the dates they had worked in that study area, and to report how the abundance of figs in their study area had changed over that period. Possible answers were a decrease of 25-50%, a decrease of 5-25%, no major change, an increase of 5-25%, or an increase of 25-50%. Answers were coded -2,-1,0,1,2 respectively. Experts were then asked to rate the confidence they had in their estimates (“very certain”, “quite sure”, “unsure”, “speculative”, or “I have only visited the study area once”). Responses rated “unsure”, “speculative”, or “I have only visited the study area once” were discarded, along with responses from experts who had worked in their study area for less than 10 years. This period was selected as it is likely to be the minimum length of time for a noticeable change in abundance to occur, as estimated by other studies of *Ficus* trees (Cottee-Jones et al., *in review*). The remaining responses (n=46) were averaged for each region.

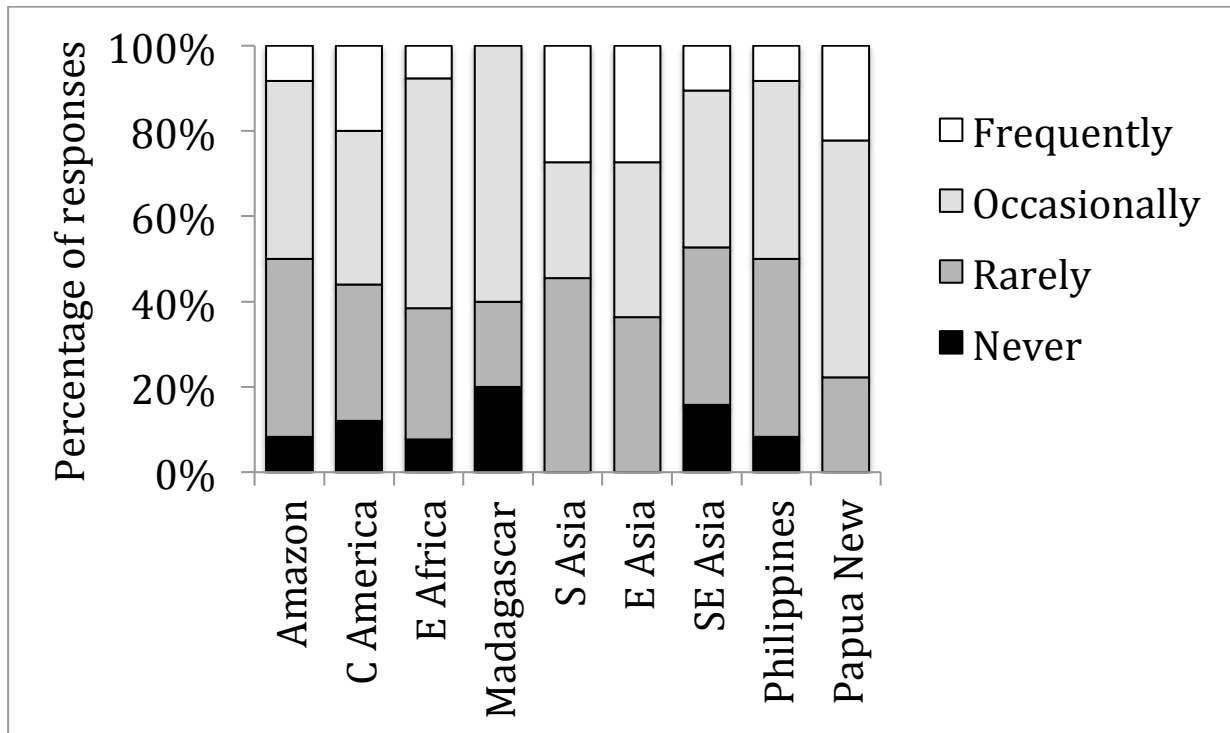


Figure 11.2: Frequency of *Ficus* felling in nine regions. Experts were asked, for a named study area, how frequently local inhabitants cut *Ficus* trees down. Possible answers were frequently (coded 4), occasionally (3), rarely (2), never (1), or unsure. Answers of “unsure” were excluded from analysis. The frequency of each response was plotted as a proportion of the total responses for each region. The number of responses for each region were: Amazon=12; Central America=25; East Africa=13; Madagascar=5; South Asia=11; East Asia=11; South-east Asia=19; the Philippines=12; Papua New Guinea=9.

Table 11.1: Reasons for felling *Ficus* trees. Experts were asked to indicate the reasons for cutting fig trees down in their study areas. Experts were permitted to provide as many reasons as necessary. 120 experts answered the question, providing a total of 216 individual responses. Responses were grouped into categories and ranked according to the number of times each was cited.

Reason	Frequency	Percentage
General land clearance	83	38.43
To minimise the extent of shade in agricultural areas	24	11.11
Wood needed for timber	24	11.11
Wood needed for firewood	19	8.80
To minimise the extent of roots in agricultural areas	18	8.33
Figs have no economic value	17	7.87
Road construction	12	5.56
To make tools	7	3.24
To protect buildings	6	2.78
For ethnomedicinal products	2	0.93
Spiritual concerns	2	0.93
To protect other trees	1	0.46
To provide fodder for livestock	1	0.46

Before conducting the PCA, the responses of respondents who answered “unsure” were excluded pair-wise from the dataset, which reduced the sample size from 144 to 54. The KMO measure of sample size adequacy produced a result of 0.64, which is above the acceptable minimum of 0.5 (Kaiser, 1974; Hutcheson & Sofroniou, 1999; Field, 2009), and all KMO values for individual items were also above 0.5 (range: 0.55–0.80). Bartlett’s test of sphericity indicated that correlations between items were sufficiently large for PCA to be conducted ($X^2_{(78)}=312.16, p<0.001$). An initial analysis was run to obtain eigenvalues for each component in the data. Four components had eigenvalues over Kaiser’s criterion of 1, and in combination explained 62.03% of the variance. The scree plot showed an inflection at component four, which would also justify retaining

these components (Supporting information C, Section 11.10). Using a critical factor loading score of 0.72 after rotation (Stevens, 2002), shade was identified as a significant item on the second PCA axis, firewood and timber loaded strongly on the third axis, and medicinal value loaded on the fourth (Table 11.2). The relationship between firewood and timber was also identified in Figure 11.3, along with an association of items pertaining to religious values. The cluster of items on particular components suggests that component 1 represents religious value (herein, Religious), component 2 relates to cultural value (Cultural), while both components 3 and 4 relate to economic value (Economic 1 and 2, respectively).

Table 11.2: Rotated factor loading scores for each question item in the four components identified using PCA. Eigenvalues and percentage of variance scores refer to factor scores after varimax orthogonal rotation. Scores in bold are those that exceed a critical factor loading score of 0.72 (Stevens, 2002). α refers to Cronbach's α , indicating the reliability of the survey results.

ROTATED FACTOR LOADINGS				
Item	Religious value (PCA 1)	Cultural value (PCA 2)	Economic value 1 (PCA 3)	Economic value 2 (PCA 4)
Food		-0.13	0.62	0.22
Fodder	0.40	0.15	0.51	0.17
Firewood		0.29	0.78	
Timber		0.15	0.75	0.11
Medicine	0.32	-0.20	0.26	0.73
Shade	0.34	0.73		0.14
Farming	-0.11	0.52		0.61
Water		0.70	0.28	-0.17
Land	0.11	0.51	0.23	0.54
Beauty		0.61		
Spirits	0.62	-0.15	-0.25	0.23
Shrines	0.91	0.14	0.15	
Temples	0.86	0.12	0.13	
Eigenvalues	2.36	2.18	2.13	1.39
% of variance	18.17	16.74	16.40	10.72
α	0.77	0.73	0.65	0.59

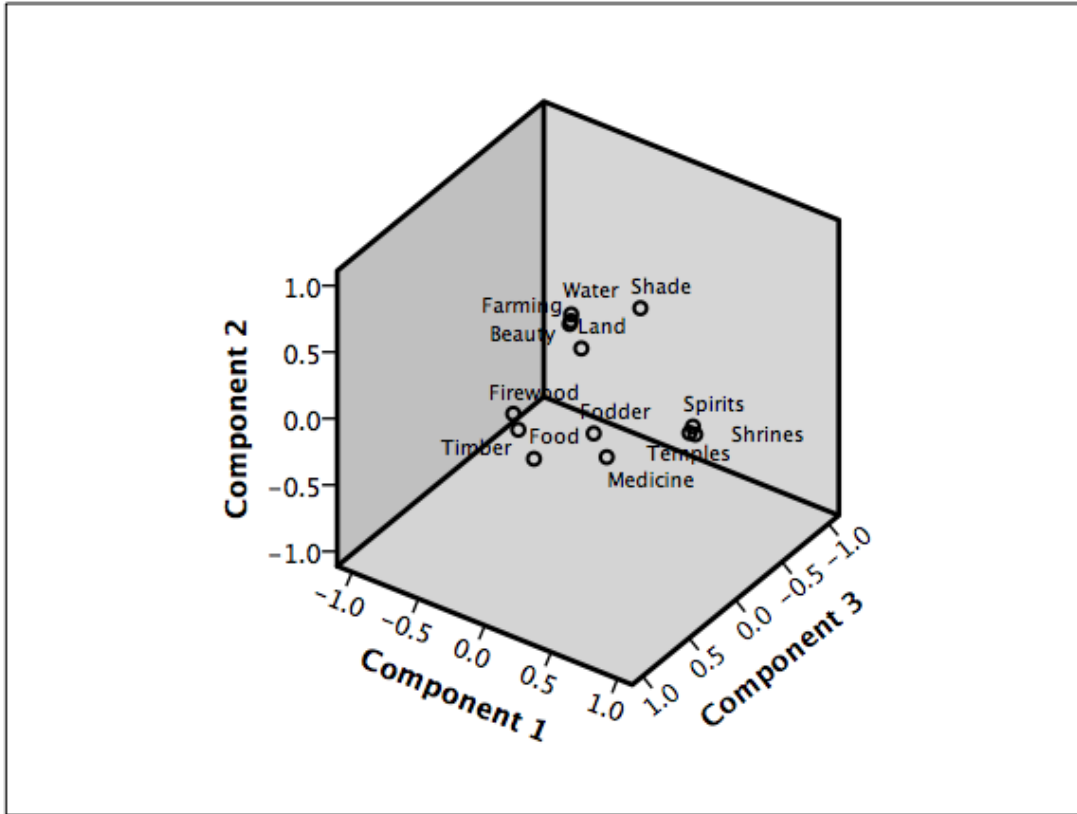


Figure 11.3: Rotated factor plot of values attributed to *Ficus* trees along three component axes. 144 experts were asked, for a specific study area, to answer 13 multiple-choice questions concerning the values local people in that study area attributed to *Ficus* trees. After “unsure” responses were excluded (reducing the sample size from 144 to 54), these survey data were coded and entered into a Principal Components Analysis. A varimax orthogonal rotation with Kaiser stopping criterion of eigenvalues greater than 1 was used, and the three components which explained the most variance (51.31%), after rotation, were plotted above. A Kaiser-Meyer-Olkin measure (0.64) and Bartlett’s test of sphericity ($\chi^2_{(78)}=312.16, p<0.001$) indicated that the sample size and correlations were adequate for factor analysis. The factor loadings and clusters in this Figure, and in Table 2, were used to approximate the identity of the factors. In this figure, the factors were judged to represent: Component 1=Religion; Component 2=Cultural; Component 3= Economic 1.

After parametric assumptions were checked, the differences in mean scores for individual components were tested across regions using ANOVA. Levene’s test indicated that equal variances could be assumed for Cultural, Economic 1 and Economic 2, but not for Religious value. The ANOVA found significant differences between both economic

components across regions (Economic 1: $F_{(7,40)}=2.47$, $p<0.05$, $r=0.55$; Economic 2: $F_{(7,40)}=4.08$, $p<0.01$, $r=0.66$), but not for Cultural values ($p=0.33$) (Figure 11.4). The Welch test for unequal variances also found a significant difference for Religious values (Welch's $F_{(7,13.34)}=11.70$, $p<0.001$). The Games-Howell post hoc test confirmed that there were significant differences between Central America versus East Africa, South Asia, and East Asia, along with the Philippines versus East Asia for Religious value. No significant differences were found between countries in the Cultural or Economic 1 components, but Hochberg's GT2 test for unequal sample sizes identified significant differences between the Amazon and Central America, and Central America and Madagascar, for Economic 2.

A reliability analysis found the overall questionnaire met the requirements for a reliable survey ($\alpha>0.7$) (Kline, 1999), with no corrected correlations below 0.3 for individual items. When individual subscales were analysed, Religious ($\alpha=0.77$) and Cultural ($\alpha=0.73$) value still recorded scores above 0.7, although both economic scores were below this threshold (Economic 1: $\alpha=0.65$; Economic 2: $\alpha=0.59$). However, all item correlations were above 0.3, and the change in Cronbach's α if an item was deleted was negligible in the two cases where this situation arose.

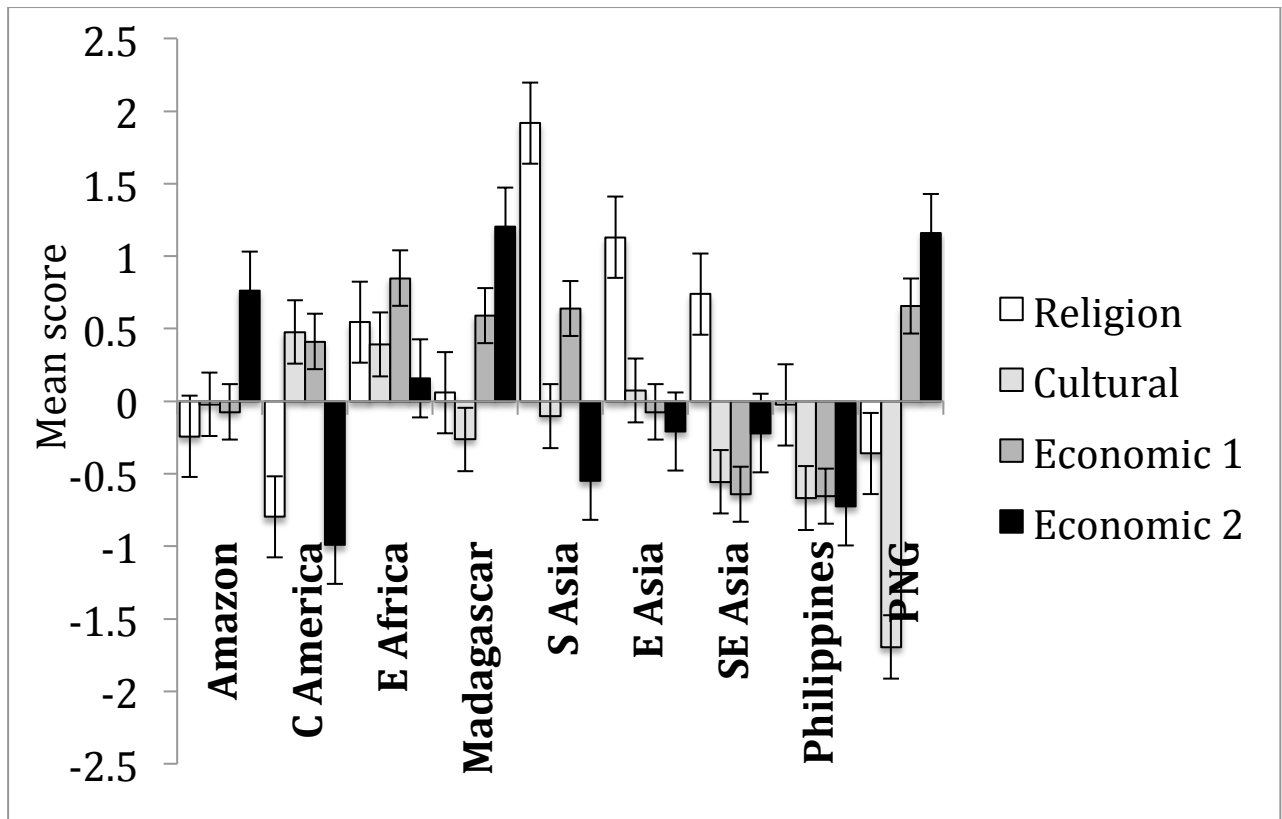


Figure 11.4: Means of the four components identified via the factor analysis, plotted for each region (Religion=PCA 1; Cultural=PCA 2; Economic 1=PCA 3; Economic 2=PCA 4). Error bars are standard error. Only one survey from Papua New Guinea (listed here as PNG) was retained in the analysis due to the frequency of uncertain responses, so the data from this region should be treated with caution.

To compare the value attributed to *Ficus* trees to other trees, we asked respondents three questions focusing on their relative economic, environmental, and cultural significance. On average, fig trees were reported to have less economic value (mean± SD=-0.51±0.13), but more environmental (0.59±0.12) and cultural value (0.73±0.13), than other trees. However, this difference was only significant for cultural values ($\chi^2_{(8)}=40.89, p<0.001$), with South Asia, East Asia, and Madagascar recording the highest mean ranks. South Asia also recorded the highest average, with 1.82 out of a maximum of two, for the cultural value of figs compared to other trees (Figure 11.5).

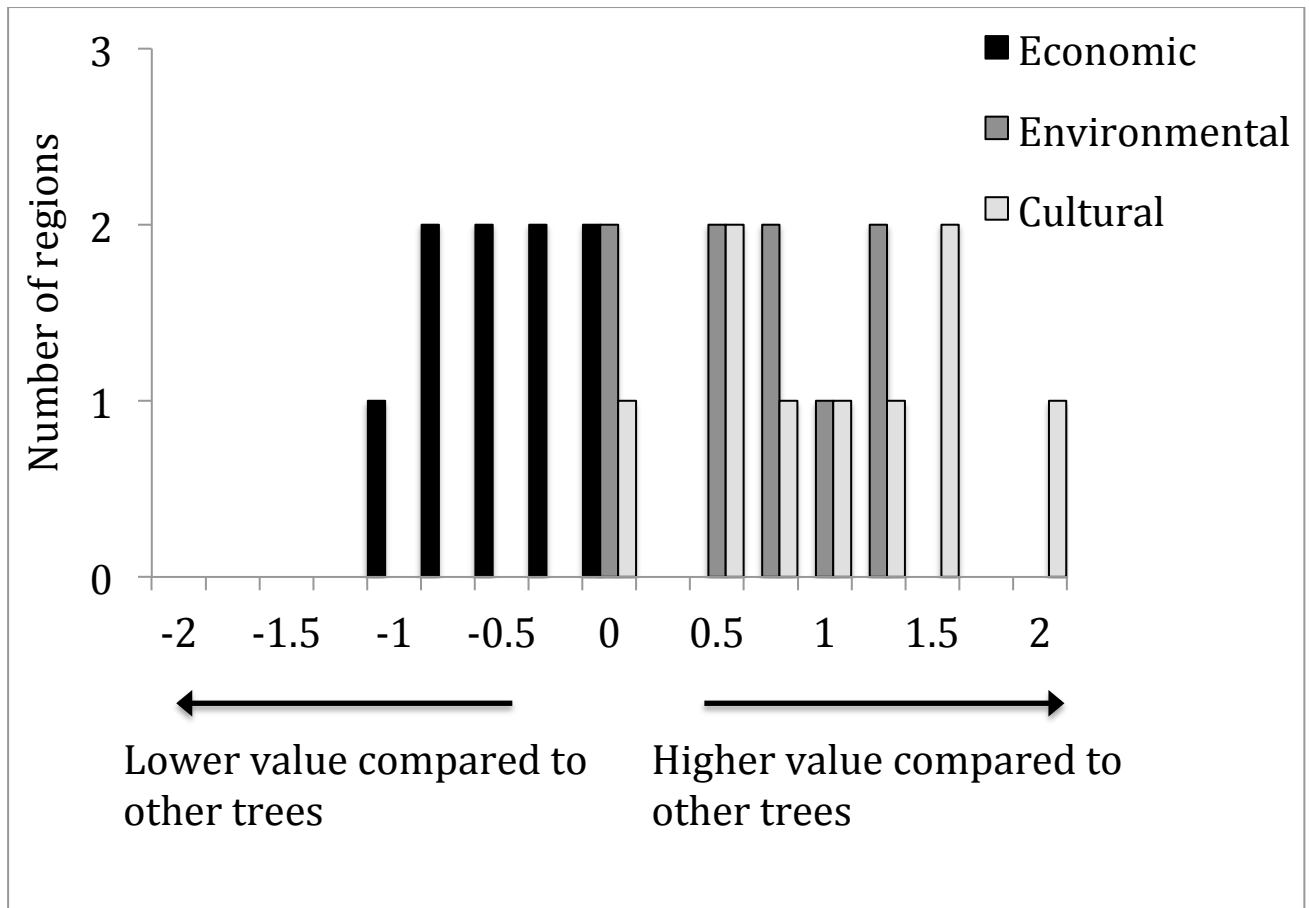


Figure 11.5: Distribution of *Ficus* values, relative to other trees, in nine regions. For a named study area, experts were asked to rate the relative value of *Ficus* trees, in comparison to other trees, in three categories: economic value, environmental value, cultural value. Possible answers were “much less” (coded -2), “slightly less” (-1), “no difference” (0), “slightly more” (1), “much more” (2). The average score was calculated for each region within each question, and the frequency of regions returning an average score in 0.25 cohorts between -2 and 2 was plotted for each value.

Fig planting was reported from all regions, although 31.50% of all respondents said that figs were never planted in their study areas (Figure 11.6). Significant differences in the frequency of fig planting were identified between regions ($H_{(8)}=28.64$, $p<0.001$), with East Asia and South Asia obtaining the highest mean ranks. Post hoc Mann-Whitney U tests between Neotropical and Asian countries found that reported fig planting frequencies in Central America were significantly lower than South Asia ($U=53$, $p<0.01$), while frequencies in the Amazon were also lower than East Asia ($U=28.5$, $p<0.02$). The

most commonly cited reasons for planting fig trees were: to provide shade, and because they are beautiful (both of which were given 36 times each) (Table 11.3). Differences in the number of times particular reasons were cited were significant ($\chi^2_{(11)}=115.39$, $p<0.001$). However, for respondents who answered with a high degree of certainty, only 23% thought that providing free fig seedlings would successfully encourage fig planting in their study area ($\chi^2_{(2)}=21.43$, $p<0.001$), while only 18% felt that providing free tree guards would be successful ($\chi^2_{(2)}=13.64$, $p<0.01$). In both cases, the majority of respondents answered that such strategies “may be successful” (59% and 48% respectively).

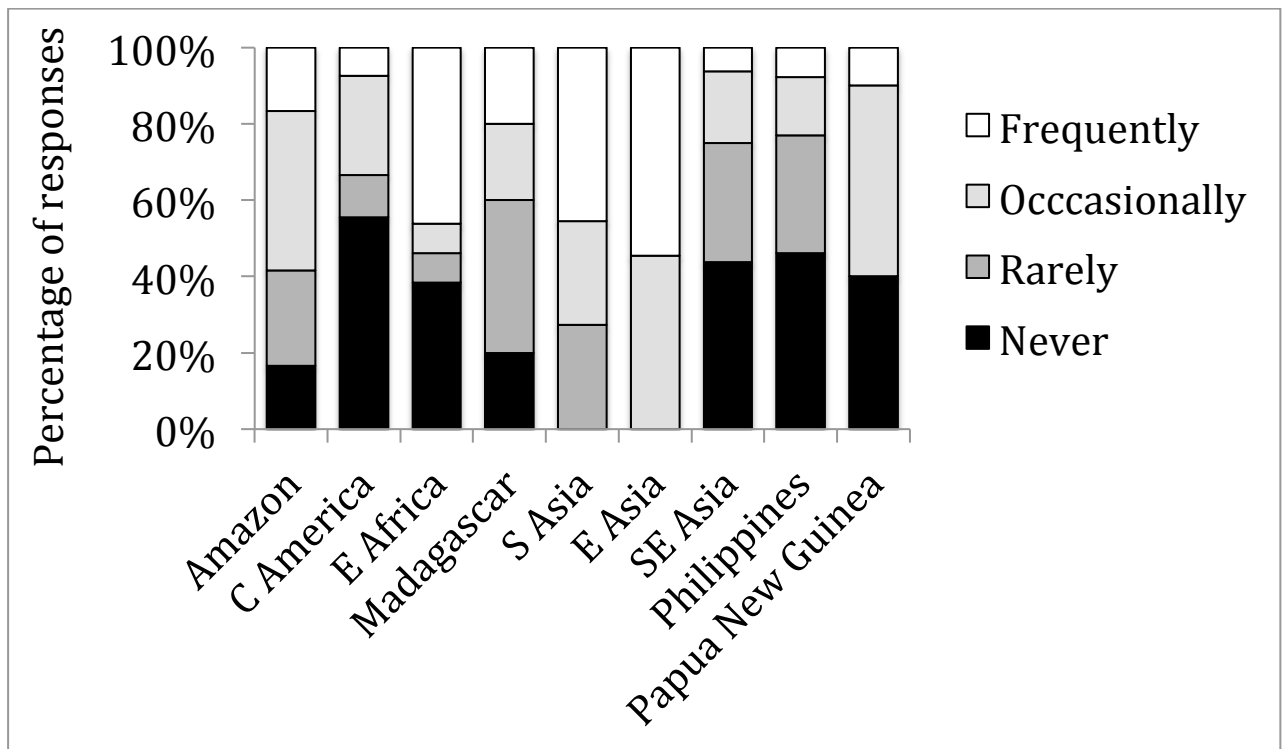


Figure 11.6: Reported *Ficus* planting frequencies in nine regions. Experts were asked, for a named study area, how frequently local inhabitants planted *Ficus* trees. Possible answers were frequently (coded 4), occasionally (3), rarely (2), never (1), or unsure. Answers of “unsure” were excluded from analysis. The frequency of each response was plotted as a proportion of the total responses for each region.

Table 11.3: Reasons for planting *Ficus* trees. Experts were asked to indicate the reasons for planting fig trees in their study areas. Experts were permitted to provide as many reasons as necessary. 89 experts answered the question, providing a total of 171 individual responses. Responses were grouped into categories and ranked according to the number of times each was cited.

Reason	Frequency	Percentage
To provide shade	36	21.05
Because they look beautiful	36	21.05
To mark a site of religious or spiritual importance	25	14.62
To mark a land boundary	20	11.70
To increase forest cover	15	8.77
To provide wood	8	4.68
To provide goods	7	4.09
To provide animal fodder	7	4.09
To help biodiversity	6	3.51
To line urban streets	4	2.34
To provide medicinal products	4	2.34
To provide barkcloth	3	1.75

11.6 Discussion

Our results imply that figs are relatively resilient to deforestation and targeted tree removal. The majority of experts believed figs were declining slower than, or at about the same rate as, other trees in their study area. In regions where they were reported to be decreasing, the rate of decrease was not significantly different from region to region. At a global scale, figs appear to have less economic value compared to other trees collectively, but more environmental and cultural value. Regionally, figs seem to have considerably more religious value in East Africa and Asia than they do in the Neotropics. In terms of increasing *Ficus* abundances through conservation initiatives, no clear message could be ascertained by fig-planting rates, although the most common reasons given for planting

figs related to environmental and cultural factors, rather than economic imperatives. The majority of respondents were equivocal as to whether providing free fig saplings or tree guards would help encourage *Ficus* planting rates in their study areas, so it may be more helpful to explore methods that rely on natural *Ficus* recruitment.

Although six of the nine regions reported decreases, these decreases were not significant. Furthermore, 92.86% of respondents said that figs were declining slower, or at a similar rate to, other trees. These findings suggest that figs are relatively robust to tree removal pressures, and may have a healthier conservation status than other ecologically important tree types. For example, large old trees, which are believed to play essential ecological roles in a range of environments, are thought to be disproportionately vulnerable to decline as a result of accelerated mortality and impaired recruitment (Lindenmayer et al., 2012; 2013). Scattered trees, which provide critical vegetation connectivity across open landscapes, and which can act as restoration nuclei in disturbed areas (Manning et al., 2006), are also predicted to decline to extinction in every landscape in which they have been studied (Gibbons et al., 2008). In the case of *Ficus*, perhaps their value to humans explains the difference between their conservation status and that of other scattered and large old trees. Tellingly, of the reasons provided for removing *Ficus* trees, the most frequently given motivation was general land clearance, which accounted for 38.43% of all reasons cited. This suggests that all trees were cut down, whatever their human-use values. Meanwhile, reasons that could be expected to be major motivations for cutting other trees down, such as the need for timber and firewood, only accounted for 11.11% and 8.80% of reasons given for figs. This may reflect the low economic value of figs, as indicated by Figure 11.5 and reports from the wider literature, which describe many species of *Ficus* as producing low-value wood that also does not burn very well (Fredericksen et al., 1999; Dutta, 2006; Felton et al., 2013).

Although lower economic value was found at a global level, there was some regional variation in the values ascribed to figs. Several authors have described ethnographical or anecdotal links between religious or spiritual faith and fig trees in East Africa, South Asia, and East Asia (Beech, 1913; Huabin, 2003; Jain & Kapoor, 2007; Wilson & Wilson, 2013), while we found scant records linking faith to *Ficus* in Central or South America (Alcorn, 1984; Lentz, 1993; Harvey & Haber, 1999). In fact, the only references we could find to such a link were the substitution of the West African Iroko tree (*Milicia excelsa*) for *Ficus* in an Afrocentric Brazilian religion (Voeks, 1997), and a possible link between ancient Mesoamerican civilisations and *Ficus* trees, as indicated by the spatial juxtaposition of figs and temples (J. Alcorn *pers. comms.*; E.M.P. Malagón *pers. comms.*). However, this could simply be a result of *Ficus* seeds finding favourable sites for germination on the temple ruins, as has been reported in India, and is widely observed on modern buildings around the world (Sitaramam et al., 2009; J. Alcorn *pers. comms.*; E.M.P. Malagón *pers. comms.*). Indeed, we found that figs scored poorly for religious value in the Neotropics, with Central America receiving the lowest mean score for religious value out of all the regions studied. Instead, our experts commented that figs had ornamental value in Central and South America, with non-native *F. benjamina* and other species planted along urban streets and in town squares for aesthetic reasons (A. Ladio *pers. comms.*). In fact, in Florianópolis, Brazil, the centre of the city is marked by the “*Figueira centenaria*” or “fig tree square”, which also provides the city’s football team with its logo and name (Figueirense) (N. Hanazaki *pers. comms.*). Some people also revered figs as they were perceived to have no flowers and yet still produce fruit, while in Mexico they had historical value as the source of the barkcloth-like “*Amate*” paper, produced from the fibres of the Amate tree (*F. petiolaris*) (Peters et al., 1987; E.M.P. Malagón *pers. comms.*).

The use of figs in barkcloth production and as important landmarks is also widespread in East Africa and Asia (Aragon, 1990; Hines & Eckman, 1993; Gaultier, 1996; Wilson & Wilson, 2013). Furthermore, our results corroborate reports from the literature referring to people in India, China, and various societies in South-east Asia and East Africa worshipping figs, or at the very least considering figs to be sacred. The strength of the link between faith and figs is particularly clear in South Asia, which recorded the highest mean score (1.92 out of a possible maximum of two) for religious values out of all the regions studied. Here, the link between figs and religion is well established, with at least two world faiths holding *F. religiosa* and *F. benghalensis* in reverence (Gadgil, 1987; Kumar et al., 2011; Caughlin et al., 2012), and numerous other reports of these species holding sacred status in India (Bhatla et al., 1984; Dutta, 2006; Teron, 2009). For example, the Mikhir of Assam, North-east India, believe that cutting or damaging a *F. religiosa* or *F. benghalensis* is as sinful as killing a holy man (Jain & Kapoor, 2007). In East Asia, the relationship between belief systems and figs is less well studied, but several authors have commented on the sacredness of *F. religiosa* and *F. altissima* (Huabin, 2003), their use as locations for traditional ceremonies and rituals (Wilson & Wilson, 2013), and the taboo on cutting large *F. altissima* trees in southern China (Long & Zhou, 2001). In East Africa, our results are consistent with the previously documented *Ficus* use in traditional practices of worship in Tanzania, Kenya, and Uganda (Beech, 1913; Hines & Eckman, 1993; German et al., 2006). The high mean scores for both cultural and economic value also indicate the importance of *Ficus* trees for barkcloth production in the region, which has been listed by UNESCO as an “Intangible Cultural Heritage of Humanity” (UNESCO, 2008).

These results imply a need for fig conservation strategy that is sensitive to differing local attitudes. Given the lack of economic incentives for fig conservation, and the abundance

of suitable substitutes in cases where they do provide material benefits, figs do not fit well within a monetised ecosystem services framework (de Groot et al., 2002; Howarth & Farber, 2002; Luck et al., 2009; Chan et al., 2012). However, our results indicate that they are consistently valued for their cultural attributes, which constitute the less tangible components of this approach to conservation. Indeed, there was no significant difference in the level of cultural value across our regions, figs were believed to hold more cultural value than other trees, and the main reasons given for planting figs were shade provision and their beauty.

In East Africa and Asia, the high religious value of figs may present a further opportunity to secure the future of *Ficus* trees. Several authors have recommended aligning biodiversity concerns with religious interests to achieve conservation goals (Palmer & Finlay, 2003; Bhagwat & Palmer, 2009; Dudley et al., 2009). They argue that religious groups are very effective at activating behavioural norms and conserving sacred sites, and so it may be possible to position figs as micro-scale sacred sites. To some extent, this would not represent a major change in attitudes towards figs in South and East Asia, and so may be readily implemented.

However, before associating fig tree conservation with their sacred status, it is important to consider the reasons why the regions with the highest mean scores for religious value in our study, South and East Asia, also recorded the highest scores for the frequency of fig removal, and why they were the only two regions where experts did not check “Never” in response to the question concerning how often local people cut figs down. It may be that attitudes towards *Ficus* and faith in these areas are more pragmatic than commonly assumed, and that even recognised sacred trees provide little obstacle in the face of economic or development incentives. Given the economic problems reportedly posed by figs (reducing agricultural productivity and damaging buildings), and the availability of

superior substitutes for the provision of firewood, timber, animal fodder, and medicinal products (alternatives are listed in Dutta, 2006 and Kumar et al., 2011, for example), it may be unwise to place too much emphasis on religious attributes when promoting the conservation of *Ficus* trees. Doing so may create a tension between economic and religious interests, and risks aligning *Ficus* conservation with a religious cause that may be undermined by economic imperatives when they come into conflict.

Furthermore, as this study has illustrated, figs do not appear to hold religious or spiritual value in the Neotropics, and the results from Madagascar, the Philippines, and Papua New Guinea are inconclusive, so it may be best to focus on cultural or economic incentives more widely. Cultural values, in particular, did not differ significantly across the regions studied, and ranked highly on reasons for planting figs. By underlining the important cultural, and perhaps ecological, role *Ficus* trees can play, community-led education campaigns may be able to garner wider support for *Ficus* conservation. Hence, an appreciation of cultural values may offer a promising approach to securing the future of *Ficus* populations.

More widely, this study provides an example of the utility of expert opinion surveys in directing conservation measures. Given the widespread and increasing extent of internet connectivity, and the wealth of knowledge held by researchers and practitioners on topics of concern around the world, it seems surprising that the elicitation and synthesis of experts opinions, as demonstrated here, is not more commonly used to assess or scope global conservation issues (Halpern et al., 2007; Donlan et al., 2010; Sutherland et al., 2011; 2012a; 2012b). As internet-based expert-opinion surveys offer the opportunity for fast and inexpensive conservation assessments, we suggest that the practice is formalised, with the creation of a database of suitable experts who could be stratified by subject of

expertise, geographical area, and taxonomic specialisation, ready to provide expedient responses to surveys of urgent conservation matters.

11.7 Conclusion

This study has quantified, for the first time, the geographical variation in social values attributed to *Ficus* trees. We found that the high religious value often associated with *Ficus* trees appears to be confined to Asia and East Africa, while economic value varied markedly between regions. Despite having less economic value compared to other trees, our experts did not report that figs were experiencing a greater decline than other trees in their study areas. This may reflect the high cultural value of fig trees, which could be harnessed to promote their conservation in the regions studied.

11.8 Acknowledgements

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11.10 Supporting information

Supporting information A

To assess whether six completed surveys were sufficient to include Madagascar in the study, we conducted a saturation analysis to determine how much new information was provided by each additional questionnaire (Lung et al., 2012; Laurance et al., 2013). We randomly selected five questions from the Madagascan survey results, and pooled the data to generate mean scores for each question. We compared these results to randomly generated data (data were generated using the R function “runif”; R Core Team, 2014), using linear regression. We compared R^2 scores after the addition of each question (Figure 11.7). The rapid and non-linear rise of the survey data, which converged on the final values after just three completed questionnaires, led us to the conclusion that six questionnaires were sufficient to capture an adequate sample of expert knowledge in this region.

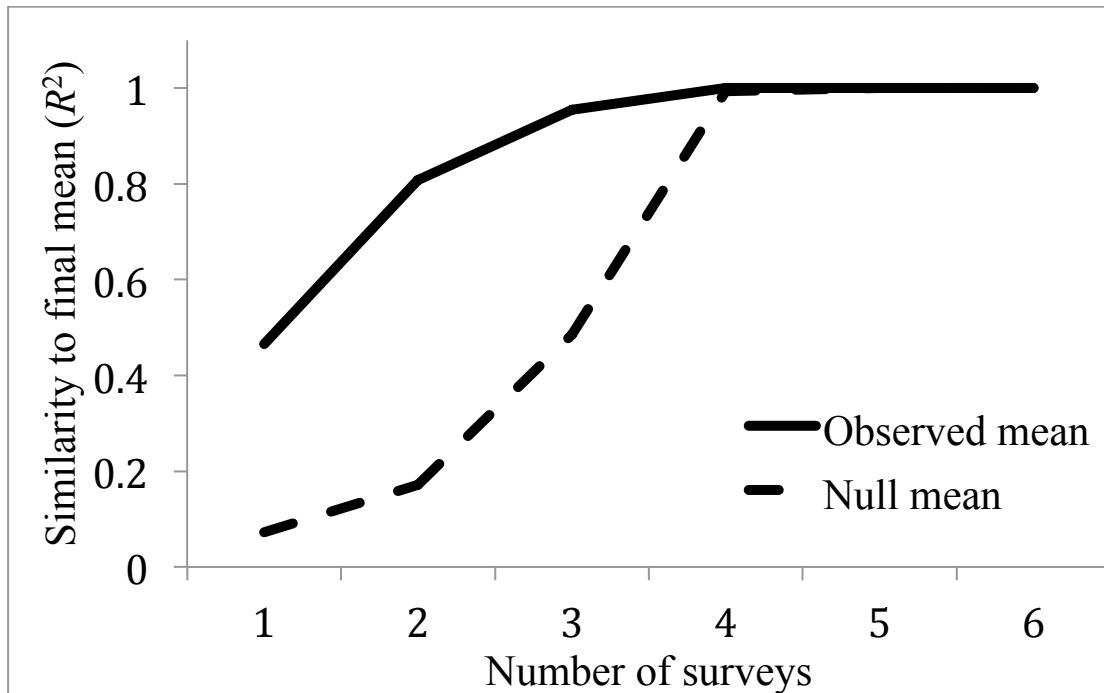


Figure 11.7: Saturation curves for the mean observed scores across five randomly selected survey questions, compared to values achieved with randomly generated data (null mean) for Madagascar. Random data were generated using the “runif” function in R, R^2 values were obtained through linear regression.

Supporting information B

Below we present a non-interactive version of the questionnaire used in this study.

Thank you for your participation in the global fig social survey (Ficus, Moraceae). Our aim is to test how community attitudes and beliefs concerning fig trees change geographically. As someone who has conducted fieldwork in an area with fig trees, we would be very grateful if you could respond to the following 36 short questions about the values these trees hold for people living in a specific field study area you have worked in. The results from this questionnaire will be used in a university study, and will not be passed on to any third parties. If you do not feel comfortable completing the questionnaire, you can stop at any time. We will start off with a few background questions.

Section 1

1) What is your name? If you wish to remain anonymous, that is absolutely fine, please leave the box blank.

Response:

2) Which sector do you work in? If you would prefer not to say, that is absolutely fine, please leave the box blank.

Academic

Not-for-profit

Consultancy

Government

Other:

3) Where is your study area? Please provide the state/province and country.

Response:

4) When was the first time you visited your study area? Please provide the year and month if possible.

Response:

5) When was the last time you visited your study area? Please provide the year and month if possible.

Response:

6) How would you describe the dominant land-use in your study area? (For example: coffee plantations, mixed agriculture, cattle pasture, secondary forest, cocoa agroforestry).

Response:

7) How has the abundance of figs changed in your study site while you have worked there?

-50 to -25%

-25 to -5%

no major change

+5 to +25%

+25 to +50%

I have only visited the study area once

8) How confident are you in your estimate of fig tree abundance changes in the previous question?

very certain

quite sure

- unsure
- speculative
- I have only visited the study area once

9) Which fig trees occur in your study area? Please list up to five of the most common species. (Scientific and/or local names will suffice).

Response:

Section 2

Thank you very much for completing Section 1. We would now like to find out more about the economic and cultural status of fig trees in your study area. Please report the dominant viewpoint held by the local inhabitants of your study area. There are 13 multiple-choice questions in this section.

1) Do people harvest food from fig trees for human consumption?

- never
- rarely
- occasionally
- frequently
- unsure

2) Do fig trees provide a good source of food for livestock in your study area?

- not at all
- not really
- fairly important
- very important
- unsure

3) Do people gather firewood from fig trees?

- never
- rarely
- occasionally
- frequently

unsure

4) Do people obtain timber from fig trees?

never

rarely

occasionally

frequently

unsure

5) Do people harvest products used in medicine from fig trees?

never

rarely

occasionally

frequently

unsure

6) Do people in your study area think fig trees provide important sources of shade for shelter?

not at all

very few

quite a lot do

everyone does

unsure

7) Is the shade provided by fig trees good for farming?

no, shade is bad for farming

not really

quite good

very good

unsure

8) Do people in your study area believe fig trees regulate water supply?

- not at all
- very few
- quite a lot do
- everyone does
- unsure

9) Are fig trees used to demarcate land ownership boundaries?

- never
- rarely
- occasionally
- frequently
- unsure

10) Do people think fig trees are beautiful?

- not at all
- very few
- quite a lot do
- everyone does
- unsure

11) Do people in your study area believe ghosts or spirits live in fig trees?

- not at all
- very few
- quite a lot do
- everyone does
- unsure

12) Are shrines built at the base of fig trees in your study area?

- never
- rarely

occasionally

frequently

unsure

13) Are fig trees found near temples or other religious buildings in your study area?

never

rarely

occasionally

frequently

unsure

Section 3

1) Do people in your study area think fig trees have more economic value than other trees?

much more

slightly more

no difference

slightly less

much less

unsure

2) Do fig trees gain more economic value as they get older?

much more

slightly more

no difference

slightly less

much less

unsure

3) Do people in your study area think fig trees have more environmental value than other trees?

- much more
- slightly more
- no difference
- slightly less
- much less
- unsure

4) Do fig trees gain more environmental value as they get older?

- much more
- slightly more
- no difference
- slightly less
- much less
- unsure

5) Do people in your study area think fig trees have more religious value than other trees?

- much more
- slightly more
- no difference
- slightly less
- much less
- unsure

6) Do fig trees gain more religious value as they get older?

- much more
- slightly more
- no difference
- slightly less

much less

unsure

Section 4

Finally, we would like to get your views on the future prospects of fig trees in your area. There are only 8 questions to go.

1) Are fig trees cut down in your study area?

never

rarely

occasionally

frequently

unsure

2) If they are cut down, why? Please list as many reasons as necessary.

Extensive shade is bad for crops

Extensive roots are bad for crops

Have no economic value

Needed for timber

Needed for firewood

General land clearance

Other (Please specify):

3) Are people in your study area more likely to cut down fig trees than other types of tree?

much more likely

slightly more likely

no difference

slightly less likely

much less likely

unsure

4) Are fig trees planted by people in your study area?

- never
- rarely
- occasionally
- frequently
- unsure

5) If fig trees are planted in your study area, why? Please list as many reasons as necessary.

- To provide shade
- To mark a land boundary
- To mark a site of religious or spiritual significance
- To provide wood
- Because they look beautiful
- To increase forest cover

Other (Please specify):

6) Would providing free fig seedlings be successful in encouraging fig planting in your study area?

- would not be successful
- may be successful
- would be successful
- unsure

7) Would providing free fencing around fig seedlings be successful in encouraging fig planting in your study area?

- would not be successful
- may be successful
- would be successful
- unsure

8) Are figs declining faster or slower than other trees in your study area?

- much faster
- slightly faster
- about the same
- slightly slower
- much slower
- unsure

That is it. Thank you very much for taking the time to complete the survey.

Supporting information C

For the PCA, we retained components that had eigenvalues over Kaiser’s criterion of 1. We also verified the use of this threshold by examining the scree plot of component eigenvalues (Figure 11.8), which showed an inflection at component 4, which was also the last component to have an eigenvalue greater than 1.

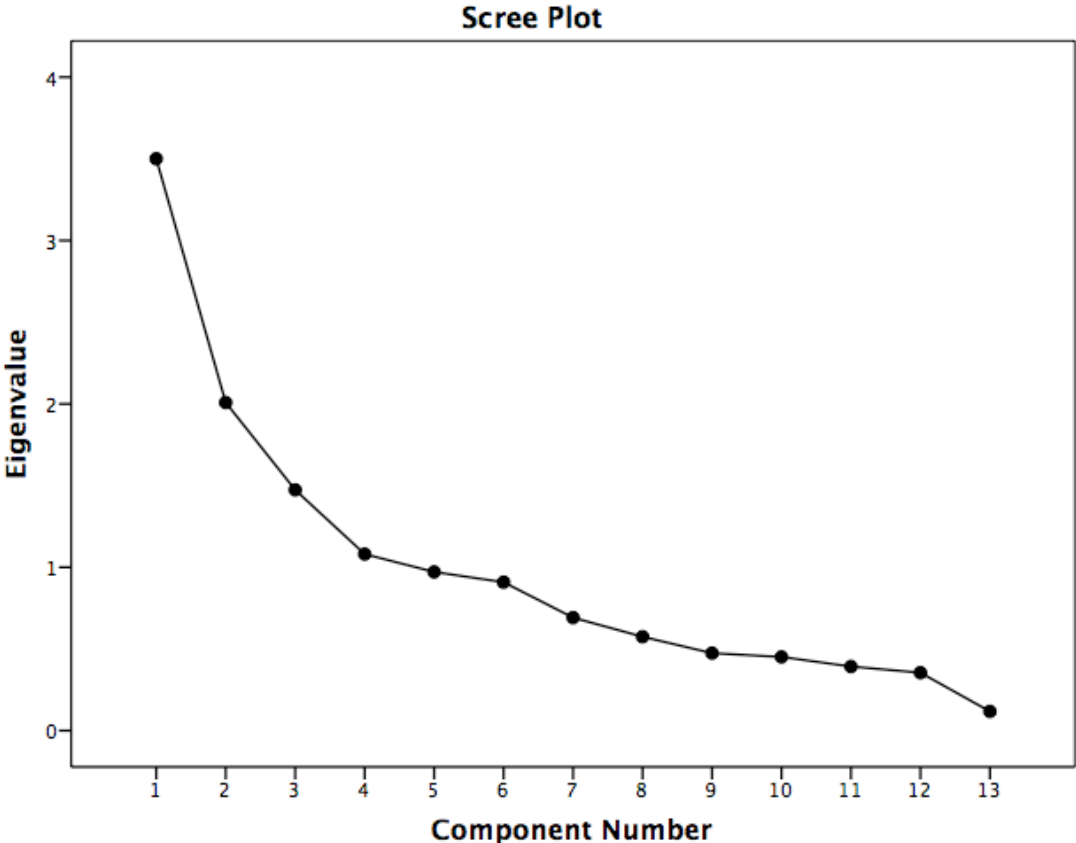


Figure 11.8: Scree plot of component eigenvalues from the PCA of human values attributed to *Ficus* trees, derived from 13 question items with 54 survey respondents.

CHAPTER 12: DISCUSSION

The previous eight chapters have addressed several pertinent conservation issues in human-modified landscapes, which can be grouped under three main themes: biodiversity conservation, ecological restoration, and the human–environment relationship. In this chapter, I assess the implications of our findings for each of these areas of research. I then consider the options for integrating *Ficus* trees into conservation agendas, before outlining the key limitations of the thesis, and discussing possible directions for future work on isolated *Ficus* trees in human-modified landscapes.

12.1 Bird conservation in human-modified landscapes

Starting with bird conservation beyond protected areas, this thesis provides four important contributions: 1) evidence for the independence of species visiting isolated trees from protected areas; 2) the relative importance of different isolated tree types for species residing in human-modified landscapes; 3) the overlooked significance of *Ficus* trees in insectivore conservation; and 4) the role isolated *Ficus* trees can play in conserving ecological function.

Previous studies of distance effects beyond protected areas or forests have surveyed isolated trees in a similar approach to this thesis (Luck & Daily, 2003; Eshiamwata et al., 2006; Brietbach et al., 2010; Lansky & Keitt, 2012; Sheldon & Nadkarni, 2013). Their results did not indicate any clear trend between bird abundance or richness and distance, with Eshimawata et al. (2006), Caughlin et al. (2012), and Sheldon and Nadkarni (2013) finding no overall relationship, da Silva et al. (1996) finding a negative relationship, Berens et al. (2008) and Lasky and Keitt (2012) finding a positive relationship, while Luck and Daily (2003) found a mixed relationship,

depending on the bird species. However, the distances investigated were often only a few hundred metres (da Silva et al., 1996; Lansky & Keitt, 2012; Sheldon & Nadkarni, 2013), and all were less than 2 km (Eshiamwata et al., 2006; Caughlin et al., 2012), except for the study by Luck and Daily (2003), who surveyed an isolated tree 8 km from the nearest protected area. In this thesis, we surveyed trees across a spatial scale that has not been attempted before. The mean distance of our isolated trees from the nearest protected area was 7.46 km, with a maximum of 32 km. This larger spatial scale provides a new perspective on the interaction between birds and isolated trees as the distance from the nearest protected area increases. Here, we found two distinct responses to increased distance depending on the life history of particular species. One group, which comprised 31.34% of all frugivores and insectivores recorded more than twice, was more dependent on forests (according to the literature: del Hoyo et al., 1992–2002; 2003–2011; Grimmett et al., 2011), and exhibited sharp declines in predicted presence in isolated *Ficus* trees within a few hundred metres. The second group (28.36%) showed greater tolerance of human-modified environments, and had a consistent or even increasing probability of occurrence in isolated *Ficus* trees as the distance from the nearest protected area increased. This finding corroborates the mixed results of earlier studies, and indicates that the characteristics of the birds involved may be the most important determinant of their likelihood to visit distant isolated trees (Luck & Daily, 2003). In studies where all species are considered as one group, the outcome is likely to reflect the dominance of forest-dependent or matrix-tolerant species, rather than any more meaningful ecological signal (Eshiamwata et al., 2006).

The greater distances studied in this thesis also suggests that those studies finding no distance effect over hundreds of metres or even two kilometres may have found a

trend if the study had been conducted at a larger spatial scale. For example, if the analysis in this thesis had been confined to those trees located within 1 km of the forest edge, there would have been no major trend in overall bird abundance between the closest quartile of *Ficus* trees and the furthest quartile (with a drop of 8.12%). However, when extended to the full dataset, the difference in abundance between the closest and furthest quartiles jumps to a decrease of 57.21%. Equally, for those studies which did identify a trend, the direction of the trend may have changed had the study been extended geographically. As an illustration, the difference in richness in the closest and furthest quartiles when the dataset is limited to those trees within 1 km of the forest is a decrease of 28.33%. When the constraint is relaxed to those trees within 8 km of the forest edge, which is the longest distance previously studied, the trend changes to a slight increase of 10.21%. Finally, when the full dataset is considered, the result is a major increase in richness, to 33.82%. (which also reflects the increased presence of matrix-tolerant species, as described above).

Few studies have examined the merits of retaining different species or types of tree in human-modified landscapes for bird conservation (Stouffer & Bierregaard, 1995; Tschardtke et al., 2011; Douglas et al., 2013). Many focus on the relationship between birds and a particular tree species, rather than comparing the strength of the relationship between trees with different attributes (Luck & Daily, 2003; Eshiamwata et al., 2006; Brietbach et al., 2010). One study that has analysed the bird communities using different types of tree in tropical human-modified landscapes is Douglas et al. (2013), where the benefits of native versus exotic trees were investigated. Their findings suggested native trees species (including *Ficus*) provide better resources for birds than exotics (reflecting the results of Macgregor-Fors and Schondube, 2011 and Helden et al., 2012). Forest-dependent species richness was positively related to

native tree cover, and regression coefficients indicated that an increase of two large native trees per hectare would increase bird densities by one bird per hectare. Of the 17 bird species recorded in their study, only three increased in density with the total number of exotic trees (Douglas et al., 2013). They also hypothesise that the number of native fruit trees may be an important determinant of forest-dependent species presence in human-modified landscapes, and comment that future work which refined recommendations for the management of human-modified landscapes for bird conservation would be a valuable area of research. In this study, we analysed the bird communities in three different isolated tree types (*Ficus*, other fruit, and large). We found that for both frugivorous and insectivorous bird species, *Ficus* trees attracted higher abundances and species richness than other tree types. This builds on recommendations to conserve native trees, and suggests that in areas where they are indigenous, *Ficus* trees may be more valuable than other fruit trees, and other trees of comparable size, in the conservation of birds beyond protected areas. If only one tree could be planted for a conservation programme, or only one tree could be saved from clearance, the results of this thesis imply that a *Ficus* tree would be the best candidate- if bird conservation were the overall aim.

The link between frugivorous birds and *Ficus* trees within forest habitats was well established prior to this thesis (Shanahan et al., 2001), but one unforeseen discovery was the strong association between insectivorous birds and *Ficus* trees. We found more species of insectivorous birds on *Ficus* trees than other tree types, and found insectivorous birds to be more abundant on *Ficus* trees. Possible explanations for this include the volume of fruit (and rotten fruit) on *Ficus* trees, the large number of fig wasps attracted to and dispersing from *Ficus* trees, and the complex bark topography of the *Ficus* species included in this study. All of these characteristics serve to create

habitat for invertebrates, so that *Ficus* trees may be rich foraging sites for insectivorous birds. This finding may be particularly important given the vulnerability of many tropical insectivores to land-use change. Numerous studies have documented the decline in insectivores within small forest blocks and in human-modified habitats beyond protected areas (Stouffer & Bierregaard, 1995; Canaday, 1997; Marsden et al., 2006; Sekercioglu, 2012). Although the insectivores recorded in this study were chiefly arboreal, our results suggest that the prioritisation of *Ficus* trees for conservation offers a promising approach to improving the feeding resources for insectivores in human-modified landscapes.

Such an approach may not just benefit resident insectivores, which were the focus of our study, but may also help conserve migratory insectivores, which are particularly vulnerable to synergistic drivers of extinction along migration pathways. We recorded 12 migratory species while surveying *Ficus* trees during seasons that were not included in the analyses in Chapter 5, including Greenish Warbler (*Phylloscopus trochiloides*), Tickell's Leaf Warbler (*P. affinis*), and Blue Whistling Thrush (*Myophonus caeruleus*). It appears likely, therefore, that *Ficus* trees may provide food resources on the wintering grounds and stop-over sites of several elevational and trans-continental migrants. An increase in *Ficus* densities in human-modified landscapes may even help arrest the decline of migrants as they travel through North-east India, while there is also some indication that *Ficus* trees may be important for insectivorous migrants in other tropical regions. In her study of fig wasp predation in Monteverde, Costa Rica, Bronstein (1988) recorded 12 species of bird that were gleaning insects off the surface of fig fruit, and assumed that the majority of prey items were likely to be fig wasps. Of these species, seven (58%) were migratory warblers that were either wintering in or migrating through the area. Further studies in

different human-modified landscapes would be useful in clarifying the significance of *Ficus* trees for migratory insectivores across a wider geographical area.

Finally, this thesis provides some of the first analyses of ecological function fluctuations following land-use change (Edwards et al., 2013), and is the first examination of ecological function at the scale of individual trees. It may also be one of the first bird studies to use solely continuous data for trait inputs, which is an important advance away from the categorical systems used in previous research, as categorisation sacrifices useful information during the classification process (Petchey & Gaston, 2006). More important, however, was the discovery that the range of ecological function in isolated *Ficus* trees (as measured by the functional dispersion index), did not collapse as the distance from the nearest protected area increased. While earlier results indicated that many forest-dependent species, including the two largest frugivores (Great Hornbill, *Buceros bicornis*, and Oriental Pied Hornbill, *Anthracoceros albirostris*) rarely venture beyond the forest edge (Cottee-Jones & Whittaker, *in review*), 92.87% of the mean functional dispersion score was retained in *Ficus* trees over 25 km from the nearest forest, compared with those *Ficus* trees within 1 km of forest. Although there is some uncertainty as to how exactly functional diversity indices should be interpreted (Lavorel et al., 2008; Hillebrand & Matthiessen, 2009; Reiss et al., 2009), the maximum gape size, which is a critical determinant of the range of seeds that can be dispersed by a community, was still 2.12 cm at 32 km distance, while at least one individual from the quartile of species with the largest gape widths was recorded at 118 of the *Ficus* trees surveyed (96.72%). This result indicates that the matrix-tolerant species, while not like-for-like substitutes, can still perform the majority of the functional role measured in trees where forest specialists were present. Although this provides encouragement that seed

dispersal networks may still function adequately in the absence of forests, further work on the dispersal distances, deposition locations, and viability of seeds consumed by matrix-tolerant frugivores may be helpful in clarifying any resultant changes in seed dispersal patterns following the loss of interaction with largest-gaped and largest-bodied frugivores.

The results of Chapters 4–6 provide further evidence that isolated trees are important ecological structures in human-modified landscapes (Manning et al., 2006). In particular, this research advances the debate by underlining the operation of distance effects over a larger scale, providing the first indication of functional resilience in communities visiting isolated trees, and identifying *Ficus* trees as especially important types of isolated tree for both frugivorous and insectivorous birds. Taken together, these findings create a body of evidence that could be the foundation for recommendations to integrate isolated *Ficus* trees in human-modified landscape bird conservation. In fact, an awareness of the role *Ficus* trees play in such landscapes may drive the adoption of novel techniques for bird conservation in tropical farmland. By supporting the land-sharing side of the debate, the conservation of individual isolated *Ficus* trees by, for instance, prohibiting their removal through either government regulation or the activation of social norms (discussed in Section 12.3 below), may bring great benefits to human-modified ecosystems, from both a compositional and functional perspective. The recognition of the importance of individual trees may help refocus conservation efforts on a finer scale, beyond conserving patches of habitat, and towards conserving micro-sites in human-modified landscapes. Conserving isolated *Ficus* trees may prove to be an extremely cost efficient conservation technique.

The small area and resource requirements needed to conserve individual *Ficus* trees, especially compared to the range and abundance of species they support, may also make them suitable foci of sustainable agriculture standards. The Roundtable on Sustainable Palm Oil (RSPO), for example, aims to reduce the negative ecological impacts palm oil (*Elaeis guineensis*) plantations have on tropical forest ecosystems (Danielsen et al., 2008; Fitzherbert et al., 2008; Bhagwat & Willis, 2009; Phalan et al., 2009). In South-east Asia, these plantations, which consist of monocultures of non-native palm trees, harbour only a tiny proportion of an area's original biodiversity, and those species that do inhabit plantations are rarely of any conservation value (Scales & Marsden, 2008). One of the main aims of the RSPO is to mitigate these negative impacts of palm oil production on biodiversity. However, despite Criteria 5.1 and 5.2 of the RSPO's "Principles and Criteria for Sustainable Palm Oil" focusing on aspects of biodiversity conservation, the RSPO admits that palm oil plantations have a very poor ecological record (RSPO, 2007). Problems cited range from a lack of commitment to a poor understanding of the terminology among those plantation managers who were willing to adopt the criteria. A special "Biodiversity Technical Committee" has been established to tackle this problem with on-the-ground solutions, such as promoting habitat connectivity and introducing forest set-asides. Given that *Ficus* trees are native to South-east Asia, and given the demonstrated role isolated *Ficus* trees can play in conserving avian biodiversity in human-modified landscapes, it seems logical, therefore, to recommend the adoption of specific *Ficus* conservation measures within this framework.

The potential use of micro-sites for conservation in tropical human-modified landscapes extends beyond *Ficus* trees to other critical ecological resources that occupy very small areas. Comparisons may be drawn to mistletoes, for example,

which are a diverse group of parasitic plants that are also distributed throughout the tropics, as well as occurring in arid and temperate biomes (Watson, 2001). They are a polyphyletic group comprising over 1,300 species in five families within the Santales (Kavanagh & Burns, 2012), which share an obligate hemiparasitic growth form. Like *Ficus*, mistletoes rely on animals, and primarily birds, to disperse the seeds presented in their fruit (Watson & Rawsthorne, 2013). In common with *Ficus*, several species of tropical mistletoe have been recorded fruiting throughout the year, providing resources during times of aseasonal fruit scarcity (Reid, 1986; Polhill & Wiens, 1998). Indeed, some mistletoes exhibit complementary fruiting phenologies, where peaks in mistletoe fruit availability coincide with local periods of fruit scarcity (Watson & Herring, 2012). These characteristics make mistletoes attractive food resources for frugivorous birds, with bird species from 66 families recorded consuming mistletoe. Given the year-round availability of mistletoe fruit in several regions at least, many species are dependent on mistletoe, including the Australian specialist Mistletoebird (*Dicaeum hirundinaceum*) (Rawsthorne et al., 2012). Other species, such as the Painted Honeyeater (*Grantiella picta*), track mistletoe availability across the vast expanses of semi-arid Australia, and synchronise their breeding with peaks in mistletoe fruiting (Oliver et al., 2003; Barea & Watson, 2007).

In another similarity to *Ficus* trees, many invertebrates feed on mistletoes, including species within Coleoptera, Diptera, Hemiptera, Homoptera, and Hymenoptera, several of which are mistletoe specialists (Hawksworth & Wiens, 1996; Watson, 2001). This raises the prospect that mistletoes may be important feeding sites for insectivorous birds, although the small size of mistletoes suggests they would not be as important as *Ficus* trees. However, they are certainly important feeding resources for nectivorous birds, several of which specialise in mistletoe, including several Australian

honeyeaters and South American hummingbirds (Aizen, 2003; Watson & Herring, 2012; Napier et al., 2014). It appears that *Ficus* and mistletoes share several ecological properties, and in particular seem to be critically important components in several study systems despite their small area requirements and scattered distribution. Furthermore, as mistletoe are also capable of prospering in disturbed landscapes (Bowen et al., 2009), it may be worth further exploring the opportunities to conserve micro-sites in human-modified landscapes, such as isolated *Ficus* trees or trees infected with mistletoes, as potentially cost efficient and ecologically effective mechanisms to conserve ecological function beyond protected areas.

12.2 Tropical forest restoration

A second field where the debate is advanced by this thesis is tropical forest restoration. Tropical forest restoration is an increasingly important topic, as agricultural areas are abandoned through shifting cultivation and emigration to urban areas (Pascual, 2005; Bowen et al., 2011; Sullivan et al., 2011). There is also considerable stake-holder interest in the topic from mining companies, which are legally obliged in several countries to restore deforested areas once mining work has been completed (Parrotta & Knowles, 2001; Lamb et al., 2005; Koch & Hobbs, 2007). Within Chapter 2, several strategies for forest restoration were discussed, including applied nucleation, monocultures, and mixed native species plantations (Lamb et al., 2005; Koch & Hobbs, 2007). It was argued that although there were considerable advantages to both applied nucleation and mixed native species plantations (Koch & Hobbs, 2007; Suding, 2011), in cases where remnant or isolated trees survived, conserving the area under and around their canopies appeared to be the most cost efficient strategy, with the added benefit of minimising the likelihood of producing an anthropologically skewed mature community.

Little work has been done, however, analysing the characteristics of remnant or framework trees that would be best placed to lead natural regeneration, other than Slocum's (2001) work in Costa Rica. In enclosed pastures, he found *Ficus* trees had the highest seed rain density, the highest density of recruits, and highest species richness, in comparison with three other species of tree (Slocum, 2001). However, the estimated volume of vegetation under *Ficus* trees was substantially lower than under two of the other three species, which was attributed to the deep shade provided by *Ficus* trees. Furthermore, unlike the other three species, Slocum did not observe tree islands forming around isolated *Ficus* trees. This was attributed to slow growth rates under *Ficus* trees, and so he argued that *Ficus* trees would not be major recruitment foci in the initial stages of succession. However, he did comment that *Ficus* trees might be more important in later seral stages, especially as they supported a greater diversity of species than the other trees studied.

Although we were unable to assess tree ages directly, the intensity of the surrounding land-use meant that the vegetation surrounding our focal trees was in effect early successional. Consistent with Slocum's Costa Rican study, we found that isolated *Ficus* trees received higher densities of seed rain, and supported higher densities and species richness of recruits than other trees. While the volume of recruits was not estimated, height was, and the saplings growing under *Ficus* trees were on average taller than those growing under non-*Ficus* trees. Although we could not control for tree age, our field observations indicated that grazing intensity probably had more of an impact on recruitment under isolated trees than tree age.

Our results differ from Slocum's in two important ways. First, we surveyed the saplings growing in a 5 m perimeter of the tree canopy, and found that the density of saplings was higher around *Ficus* trees than non-*Ficus* trees. This conflicts with his

observation that *Ficus* trees did not seem to be forming tree islands, which may be a consequence of the different survey methods used. Second, Slocum hypothesised that the communities growing under *Ficus* trees would be dominated by late-successional and frugivore-dispersed plant species. However, our species diversity and evenness estimators indicated that the communities growing beneath *Ficus* trees were comparable to those growing beneath other trees. This allays concerns that *Ficus* trees may create non-analogue communities of closely associated plants, as instead they appear to simply support richer representations of the surrounding plant assemblage.

The implication of these findings is that, in Assam at least, conserving *Ficus* trees to facilitate restoration may be an effective strategy. Even in situations where isolated *Ficus* trees were situated many kilometres from the nearest forest, seed rain densities under isolated trees did not decrease, which suggests they may be useful recruitment foci even in situations where there are no major forest seed sources present in the landscape. Given the higher richness, density, and height of recruits recorded under and around *Ficus* trees compared to non-*Ficus* trees, this study would support the preferential conservation of isolated *Ficus* trees over other tree species. At the very least, the impact of grazing pressure on recruitment densities ought to be mediated to encourage regeneration. As the area under *Ficus* trees is rarely productive agricultural land, due to the dense shallow root networks and deep shade of these trees, there would be little opportunity cost to agricultural landowners if the area around *Ficus* trees were fenced off (Dhanya et al., 2013). In Assam, effective fences are commonly constructed at negligible prices using bamboo poles. These poles are split into four sticks of approximately 1.5 m length, and cost INR1 (1 India Rupee is worth the equivalent of 1 pence in British Pound Sterling). By weaving sets of these sticks together in a grid, locals quickly construct livestock fences at very little cost.

However, they are yet to be used to fence off the area around *Ficus* trees. If such a practice could be established, these fences could even be periodically erected or removed to permit some grazing if necessary, such as the weeks following goat or cattle calving, and still substantially improve recruitment (Fischer et al., 2009).

Although this approach would have to be farmer led, and would require numerous stakeholder meetings with small-scale farmers, other strategies may also be effective at larger scales. Several of the large commercial tea plantations in Assam are certified by the Rainforest Alliance, which aims to deliver sustainable tea production (<http://www.rainforest-alliance.org/work/agriculture/tea>; accessed: 17/07/2014). This scheme was launched as recently as 2007, and follows the protocols devised by the Sustainable Agriculture Network's standards (SAN, 2010). These standards aspire to improve the ecological conditions present on the agricultural land of plantations that are members of the scheme. One of the criteria to meet the standards and achieve certification is Criterion 2.1, which dictates that a conservation program must be established, and that this "program must include the restoration of natural ecosystems or the reforestation of areas within the farm that are unsuitable for agriculture" (SAN, 2010:19). Our results provide evidence to support the use of *Ficus* trees for this purpose, and in light of our findings, it may be worth including an additional criterion in the standards that emphasises the importance of conserving *Ficus* trees on agricultural land for both tree recruitment and bird conservation.

12.3 The human–*Ficus* relationship

A third thematic area this thesis informs is that of human–*Ficus* interactions. The relationship between people and *Ficus* has been a long-standing subject of interest, and the topic is once again receiving attention in the academic literature (Lansky et al., 2008; Wilson & Wilson, 2013). This thesis contributes new evidence of the

material benefits *Ficus* trees and the plant assemblages growing beneath them provide for local human communities, analyses in depth the manifestations of the sacred status of *Ficus* in rural Assam, and examines the global distribution of these beliefs for the first time. Taken together, these findings provide new insights into the delicate trade-off between economic and cultural incentives in attempts to gain wider support for conservation measures by aligning them with religious beliefs (Palmer & Finlay, 2003; Bhagwat & Palmer, 2009; Bhagwat et al., 2011).

Not only do *Ficus* trees support plant communities under their canopies that are richer and denser than other trees, but these recruits are also valuable providers of a range of goods for the rural residents of Assam. Although the range of economic resources provided proportionally reflects the higher species richness of *Ficus* recruits, the overall effect is still one that increases the availability of these products. The plants we recorded under *Ficus* trees in Assam provided local remedies for a range of ailments, from diarrhoea to malaria, which people regularly used to treat illnesses (Dutta, 2006). Given the expense of kerosene fired cooking (Gupta & Ravindranath, 1997; Pohekar et al., 2005), and the difficulties associated with refilling canisters (which are still extremely heavy when empty, and have to be taken by bicycle to the nearest refilling station, which can be many kilometres away), wood is still the primary source of cooking fuel in the study area. However, extensive deforestation means firewood is increasingly hard to acquire, and so small islands of wooded vegetation, as we found at greater densities and heights beneath *Ficus* trees, are of great value to local households. The natural provision of these products, and their use by the local community as subsistence goods, obtained at little to no cost, may be a considerable economic and humanitarian asset in Assam.

The provision of useful plant resources has also been studied in the context of sacred groves in India, which are conserved primarily for religious reasons, although the utilitarian attributes of such groves have also been stressed (Gadgil et al., 1993). For example, the taboos that govern sacred sites in India often permit the collection of animal fodder, fuel wood, and medicinal products, creating a significant economic resource for local communities (Hughes & Chandran, 1998; Bhagwat & Rutte, 2006). In a study in North-east India, 80 medicinally important woody species were identified in two sacred groves, with the most abundant individual species occurring at 0.04 individuals/m² (Laloo et al., 2006). Although our sample area was considerably larger (57,285 m² compared to 7,740 m²), we found a similar number of medicinally and economically important species growing under isolated *Ficus* trees (84). Notwithstanding the difference in sampling effort, or that the volume of goods produced may be important, these findings suggest that a comparable range of useful plant species can be supported by individual *Ficus* trees as were discovered in two sacred groves covering 120 ha. This implies that a more efficient method of providing a range of these resources may be the conservation, for human-use, of the area and plants growing under isolated *Ficus* trees.

The common perception of *Ficus* trees in North-east India, and India as a whole, is that *F. religiosa* and *F. benghalensis* are sacred trees (Gadgil & Vartak, 1973; Sitaramam et al., 2009; Wilson & Wilson, 2013). Our ethnographic observations confirm this view, with widespread reports of *Ficus* trees having sacred status, supported by frequent observations of the creation of shrines at the base of *Ficus* trees. Indeed, in their survey of part of our study area, Barua et al. (*in prep*) found 14.65% of all mature *Ficus* trees in the area had shrines or temples associated with them. However, the reasons we heard for the sacred status of *Ficus* trees were

somewhat confused, with different informants claiming they were inhabited by spirits, ghosts, a particular God, or Gods in general. Furthermore, opinions differed as to whether they were revered due to associations with Hinduism or local faiths, while some atheistic informants claimed only old-fashioned people believed Gods lived in *Ficus* trees. Indeed, aesthetic and utilitarian values were frequently attributed to isolated *Ficus* trees, with their beauty and the provision of a cool shade described as important properties.

It seems likely that a combination of these attributes – religious, aesthetic, and utilitarian – have played a role in shaping the abundance and distribution of *Ficus* trees in this part of rural Assam. Of all *Ficus* trees mapped, 64.81% were located on roadsides, while many more were focal points of village markets. At one point along the N37, a major highway that runs across the northern part of the study area, a temple had been built amongst a roadside grove of *Ficus* trees, where buses and trucks travelling the highway stopped to pray and give an offering for their safety while they drove along Assam's dangerous roads.

The sacred status of figs supposedly prohibits the felling of *Ficus* trees in the area. This religious association is likely to have increased their relative abundance in the landscape compared to other trees which are not afforded the same taboo, and which may also bring further benefits to avian richness and abundance in the area. In this sense, *Ficus* trees may be ready-made flagships for biodiversity conservation, as they are already viewed as cultural flagships (Bowen-Jones & Entwistle, 2002). Strategies that reinforce inherent cultural associations or religious beliefs in community-led conservation projects are more likely to be effective, especially if the flagship has symbolic links to local cultural identity (Posey & OCEES, 1999; Bowen-Jones & Entwistle, 2002). In the study area, the existing taboos and attitudes towards *Ficus*

trees appear already to mimic the legislation that would be needed to formally safeguard their protection. Furthermore, many locals are also aware of the link between *Ficus* and biodiversity, as they regularly reported large numbers of birds and bats visiting fruiting figs. There were also numerous comments pertaining to a desire to help nature in the study area, with increasing tree cover seen as an important goal not just for biodiversity, but for human health and well-being too. Further work, which conducts a market-based analysis to assess the suitability of *Ficus* trees as conservation flagships in human-modified areas of Assam, may meet greater local approval than the existing protected area centered flagships (including the Asian Elephant and Indian Rhinoceros, *Rhinoceros unicornis*), which have been elected by external groups, and which cause a great deal of conflict with agricultural communities (Heinen & Shrivastava, 2009; Barua et al., 2010).

Despite the widespread reports of their sacred value, and the taboo over removing *Ficus* trees, we also found evidence that *Ficus* trees were cut down if they presented a major economic constraint, or an obstacle to development. For example, a conservation researcher admitted cutting a *Ficus* tree down in his garden, as the shade it gave prevented him growing crops successfully, while a café owner also commented that the tree between his café and the road was due to be cut down so the NHAI (National Highways Authority of India) could expand the road. On the same highway that drivers stopped to pray at *Ficus* temples, the N37, a section beyond the study area to the West had recently been expanded into a dual carriageway. As a result, all the figs which were reportedly present before the infrastructure work began had been cleared. These cases foster a concern with becoming overly reliant on the sacred nature of *Ficus* trees to promote their conservation.

While the overwhelming majority of informants felt *Ficus* trees were sacred, these beliefs may diminish should secularism succeed religion as Assam develops economically (Weber, 1905; Wilson, 1966; McCleary & Barro, 2006), or any other societal change serve to antagonise values which are currently complementary. Furthermore, the evidence suggests that even where *Ficus* trees are strongly thought to be sacred, economic incentives appear to trump religious interests. These concerns should be given careful consideration before aligning a conservation strategy with faith systems, even if the ethical issues of misrepresenting the true motivation for a conservation initiative are ignored. While *Ficus* trees may emerge to be more popular flagships than the existing options, it is important to consider them as flagships in their own ecological right, without offhandedly placing too much emphasis on their religious significance. If not, there is the risk that *Ficus* trees may be positioned with a losing cause.

Furthermore, aligning the ecological and religious attributes of *Ficus* trees to help promote their conservation would only work in a limited geographical area. Our survey of *Ficus* experts around the world established that *Ficus* species have particularly high religious and spiritual significance in East Africa, South, East, and South-east Asia, while they have almost no religious significance in the New World. Earlier authors had suspected such a pattern might exist (Caughlin et al., 2012), but this is the first study to quantitatively verify a distinct configuration in the social properties of *Ficus* at a global scale.

While the high religious value reported in Asian countries was not surprising, the correlation between high religious value and the high frequency of felling *Ficus* trees was unexpected, and further confirms the practical approach to conserving sacred trees outlined above. Fortunately, the survey also indicated alternative options for

Ficus tree conservation that may be more robust than evoking religious or spiritual doctrines. The survey found that people around the world value *Ficus* trees most for cultural and environmental services, such as their aesthetic beauty and provision of shade to shelter under. The position of old *Ficus* trees in many historic markets, squares, and road junctions observed in Assam and reported by the participating experts around the globe suggests that these attributes may have been valued for a considerable length of time. Rather than trying to provide new reasons to conserve *Ficus* based on the meager financial benefit some of their products may provide in local contexts, it may be more effective to return to ancient, widely, and deeply held notions of the significance of *Ficus* trees, and promote their conservation for reasons that have always been valued, and which are recognised worldwide.

12.4 Implications for conservation in India

In Assam, and India as a whole, the large and expanding human population is placing increasing pressure on land usage (Gadgil & Guha, 1993; Semwal et al., 2004). In the lowlands and floodplains, some of the highest population densities in the world leave very little space for wildlife (data.worldbank.org; accessed: 16/07/2014). Almost no lowland forest exists beyond the protected area system in Assam, and there is no realistic scope for creating substantial new protected areas in this densely settled region. At the same time, we heard reports of growing concerns about human health and well-being, along with fears surrounding the loss of tree cover and “nature” from the Assamese countryside. Set against these challenges, traditional approaches to conservation offer few solutions.

The main conservation tool, the establishment of protected areas, has already been exhausted. Even in those that do exist, there are frequent disputes along the boundaries with landowners, persistent human-wildlife conflict, and rampant

poaching of endangered species (Heinen & Shrivastava, 2009; Martin et al., 2009; Lopes, 2014). Without the option of expanding the protected area network, a second, and frequently employed tool, is the de-intensification of land-use beyond protected areas (Fischer et al., 2008; Brussaard et al., 2010; Tschardt et al., 2012; Fischer et al., 2014). Reducing the intensity of land-use, in particular in agricultural regions that have been subject to ecologically destructive policies, has been a major aim of conservationists in Europe and North America (Rabbinge & Van Latesteijn, 1992; Donald et al., 2001; Kleijn et al., 2003; Scherr & McNeely, 2008; Delbaere et al., 2014; Evans et al., 2014; Pe'er et al., 2014). Many of the land-sharing initiatives proposed, such as the reformed Common Agricultural Policy, are supported by publically funded subsidies, and result in only minor decreases in productivity (Pe'er et al., 2014). However, transferring such an ideology to India, where productivity is still relatively low, and where the government has no history of sponsoring such a scheme, may be difficult (Ghatak & Roy, 2007). More importantly, in a country that ranks 94th out of 119 on the Global Hunger Index (www.wfp.org; accessed: 17/07/2014), reducing productivity in the name of conservation would be an unacceptable trade-off.

Instead, conservation practitioners would be well placed to identify strategies that do not carry an economic cost, yet still provide tangible benefits to biodiversity. In Assam, the conservation of isolated *Ficus* trees may offer exactly this kind of opportunity. In their call for greater attention to the conservation status of human-modified tropical landscapes, Chazdon et al. (2009a) stressed that further research was needed in three major areas: biodiversity, restoration ecology, and human–environment interactions. Although this thesis exclusively focuses on one genus of tree, we have been able to develop a novel line of research in each of these areas, as

well as assessing approaches to conservation that cover their three key conservation concerns: the effect of landscape structure on biodiversity conservation, the provision of ecosystem services, and the sustainability of rural livelihoods. Our results provide evidence that conserving isolated *Ficus* trees can deliver favourable outcomes in all three of these areas. We therefore recommend that conservation organisations explicitly promote the preservation of isolated *Ficus* trees in Assam, and given the strong interactions with frugivorous birds in tropical forests almost wherever they are native, elsewhere as well.

Conserving *Ficus* trees, and restricting the grazing of livestock around them, is likely to incur a minute cost in comparison to other conservation schemes, and looks set to deliver a host of benefits to the composition of avian assemblages in landscapes without protected areas, seed dispersal and pest control functions in human-modified landscapes, forest restoration, the provision of economically and medicinally useful plant resources, and cultural values. While our population models suggest that *Ficus* trees are likely to persist in the study area over the long term, isolated *Ficus* trees, like other scattered trees in human-dominated landscapes around the world, are particularly vulnerable to adult mortality (Gibbons et al., 2008; Gibbons et al., 2010; Le Roux et al., 2014). Conservation measures which safeguard mature *Ficus* trees from being felled would therefore be particularly helpful in ensuring the survival of *Ficus* populations, and consequently delivering the full array of ecological and humanitarian benefits described above.

12.5 Key limitations

Like many field-based ecological projects, limitations in time and funding may have constrained the power of some of the analyses presented herein. The main component of the fieldwork for this thesis was the collection of avian visitation records to isolated trees. Over two field seasons, 128 isolated trees were surveyed for three hours each, totalling 384 hours of observation. Although the unpublished study led by Maan Barua surveyed 58 trees (and was incorporated into Chapter 4 to bring the total number of *Ficus* trees to 122), the largest sample size for a similar study in the published literature is 55 isolated trees, surveyed by Lasky and Keitt in Brazil (2012) (although their survey length per tree was only 30 minutes). Unless any unknown larger study exists, the sample size for this component of the thesis was over double the previous largest. We therefore argue that this sample size provides a good foundation to study this system in an attempt to advance the field of conservation in human-modified landscapes.

The use of experimental controls may have enabled a more definitive conclusion about the importance of fig trees, especially if the bird community in the landscape could have been surveyed both before and several years after the removal of isolated *Ficus* trees from the landscape. Aside from insufficient time, environmental and ethical concerns presented a genuine impediment to such an approach in this thesis. However, some reasonable alterations to the fieldwork methods may have helped to improve the reliability or accuracy of the results. Three potential modifications are considered here.

First, there is some debate over the best way to measure the quality of matrix habitats (Prevedello & Vieira, 2010). For Chapters 4–6, we qualitatively judged the intensity of human-land-use surrounding each focal tree as an indication of habitat condition.

Although a crude measure, it was consistently applied, and did capture the major differences between those focal trees situated at road junctions or in rice paddies, and those in overgrown village home gardens or near the forest edge. However, additional or alternative measures of matrix quality may have provided a higher resolution to our assessment of the ecological attributes of the habitat in the immediate vicinity of our focal trees. For a more rigorous method to quantify the degree of habitat suitability around focal trees in the matrix, it may have been useful to follow Fischer and Lindenmayer (2002). In their study of birds using isolated trees in rural Australia, they used aerial photographs to calculate a crown cover index of canopies within a 100 m radius of their focal trees. If high-resolution aerial photographs of the study area could have been obtained, it may have been possible to replicate this method and include the index scores as an explanatory variable for the frugivore and insectivore models. However, even this method does not account for differences in other characteristics of the vegetation surrounding focal trees, or how the value of different surrounding trees may vary according to the ecology of individual bird species.

In Chapter 9, the accuracy of the *Ficus* population simulations was constrained by two critical deficits: reliable information on the maximum age *Ficus* trees can live to, and reliable information on the age of trees that were measured in the field. A lack of research on either subject meant that we were reliant on the reports of local landowners, whereas better estimates would have improved the maximum tree age model parameter and the tree age–DBH model. However, neither maximum tree age nor growth rate were identified as important determinants of *Ficus* population density by our sensitivity analysis. Furthermore, other studies report very similar findings: tree age and growth rate were not found to be important input parameters in forestry concessions, nature reserves, or urban settings in Australia (Gibbons et al., 2010; Le

Roux et al., 2014). Therefore, although there is scope for improvement in this area, we do not believe this issue undermines the accuracy of our projections.

The global *Ficus* social survey, for the first time, brought the worldwide knowledge and expertise of *Ficus* researchers to bear on a research question. While this is a major achievement of the thesis, it is not the best way to approach the research question considered. If funding and time had permitted, a series of local studies replicating the questionnaire approach of Barua et al. (*in prep*; Appendix 3) would have been able to elicit a direct response from particular communities in the study countries, rather than on relying on an intermediary to report their attitudes towards figs. Although this may have improved the accuracy of the results, the correlation between Barua et al.'s findings and our results from India, along with the extensive experience and detailed knowledge held by many of our experts, suggests that this online approach was a justifiable method to scope attitudes towards *Ficus* trees at a fraction of the cost of multiple on-the-ground questionnaires around the world. Aside from these limitations, there are some promising areas for future work on the topics covered in this thesis, which are outlined below.

12.6 Future directions

There are three main areas where further work could build on the findings of this thesis, and improve the effectiveness of conservation strategies in human-modified landscapes. The first is bird conservation. Although the results from Chapter 4 provide convincing evidence that forest-dependent frugivores rarely forage in human-modified landscapes, catching and tracking the movements of individual forest-dependent birds at high spatial and temporal resolution may be very illuminating and add further value to this conclusion. If any patterns could be discerned, it may be possible to identify measures that could encourage forest interior species to forage at

isolated *Ficus* trees, or it may be possible to determine whether these species visit isolated figs more frequently on a seasonal basis, particularly during times of general fruit scarcity in forest food resources, for instance. The reaction of individual birds to habitat change could also be tested experimentally. For instance, in cases where forest-dependent birds visited isolated figs that were loosely connected to forest blocks by low-intensity land-uses, it would be useful to quantify how the frequency of visits changed following vegetation clearance, and what kind of restoration techniques would be most effective in increasing visitation frequencies. Aside from forest-dependent birds, it would also be interesting to track the movements of different matrix-tolerant species, such as bulbuls, starlings, and green pigeons. Comparing the distances travelled to fruiting figs, and determining whether certain species fly directly from one fig to another, would be valuable in assessing seed dispersal properties in human-disturbed landscapes. Satellite tracking, which would facilitate the kind of remotely sensed data collection that would enable the study of these questions at high resolution, offers a very promising technological approach (Robinson et al., 2010). If tall enough nets could be erected in front of fruiting *Ficus* trees, catching frugivores would not be impractical. If the cost of satellite tracking systems decreases, and the spatial resolution and frequency of location transmissions improves so that birds can be detected moving between individual trees, this may soon become a viable conservation science project (Mueller et al., 2014).

A second area within bird conservation, and one that is already starting to benefit from the advances satellite tracking technology can bring, is the use of *Ficus* trees as “fuel-stops” during migration. During the fieldwork conducted for Chapter 5, several migratory insectivores were observed feeding in isolated *Ficus* trees. A further study, designed with this information in mind, may be well placed to more fully investigate

the significance of isolated *Ficus* trees and their insect populations for migratory insectivores along major migration flyways, stop-over sites, and wintering grounds.

Finally, while collecting data on the birds visiting *Ficus* trees, numerous bird nests were also discovered in our focal trees. The size of *Ficus* trees made them suitable for large species which nest arboreally, including waterbirds and raptors. Indeed, one *Ficus* tree in the study area hosted an active Woolly-necked Stork nest (*Ciconia episcopus*), despite the species' rapid decline in India. The complex bark topography of many figs also creates numerous hollows, which are utilised by hollow-nesting species, such as the Rose-ringed Parakeet (*Psittacula krameri*) and Indian Roller (*Coracias benghalensis*), along with roosting owls, where our field observations included the Barn Owl (*Tyto alba*) and Asian Barred Owlet (*Glaucidium cuculoides*). A study that took seasonal nesting patterns into consideration may fairly quickly be able to assess the relative importance of isolated *Ficus* trees for breeding birds in human-modified landscapes, and in particular for large or specialist breeders, which may be limited by the availability of suitable breeding sites (Wilson & Wunderle, 1993; Wiebe, 2011).

Aside from birds, interesting questions concerning *Ficus* pollination and reproduction await to be investigated by researchers with specialisations in entomology, botany, and genetics. Just as the changing nature of the relationship between frugivorous birds and *Ficus* trees between forest and human-modified landscapes had been overlooked, so too have several issues surrounding the relationship between fig wasps and *Ficus* trees. For instance, several studies have examined the height and temporal characteristics of fig wasp flight profiles in tropical forests, providing important insights into how a tiny insect, with limited in-flight directional ability, no feeding organs, and a life-span of less than three days, can cover many kilometres to find a

Ficus tree ready for pollination (Compton et al., 2000; Harrison, 2003; Compton et al., 2005). Indeed, one paternity analysis discovered that *Ceratosolen arabicus*, the host-specific pollinator of *F. sycomorus*, could travel over 160 km between trees in Namibia (Ahmed et al., 2009). However, no work has been conducted on the flight profiles of fig wasps in deforested tropical landscapes, with the closest being Compton et al.'s (2005) comparative study of logged and unlogged forest in Malaysia, or Jeevanandam and Corlett's (2013) study of fig wasp flight heights in urban Singapore. In deforested landscapes, fig wasps cannot take advantage of a strong airflow above the canopy, and the consequences of this for the pollination and genetic connectivity of *Ficus* and fig wasp populations in human-modified landscapes, including rural Assam, are an important area for further study. Another approach to this issue, which would have more of a *Ficus* than Agaonid focus, would be a broad scale *Ficus* paternity analysis. A study that followed a similar approach to Lander et al.'s (2010) investigation of genetic connectivity in *Gomortega keule* (Gomortegaceae), an endangered Chilean tree, may make considerable progress on this subject. Like the *Ficus* populations encountered in this thesis, *G. keule* is insect pollinated, and occurs in forest and non-forest habitats. There, genotyping DNA from leaf, cambium, and seed samples in a paternity analysis revealed that the insect pollinators of *G. keule* travel beyond forest patches and further than at least 6 km to reach other mature trees. Pollen was also moved both from forest sites to isolated trees, and from isolated trees to forests, indicating that the fragmentation of the forest landscape had not led to the genetic isolation of individual trees, and that all trees were still contributing towards genetic interchange. In the Golaghat District of Assam, the density of certain *Ficus* species (such as *F. benghalensis*, *F. rumphii*, and possibly *F. microcarpa*) and the ease of locating them (indeed their locations have already

been mapped as part of this thesis), mean that a similar study should be feasible, and may provide interesting insights into both *Ficus* breeding biology and the conservation of isolated trees in human-modified landscapes.

A third approach to build on the results of this thesis would be to extend the geographical and contextual scope. A major and increasing threat to biodiversity in South-east Asia is conversion of tropical rainforest to palm oil plantations (Sodhi et al., 2010; Wilcove et al., 2013). Measures meant to ameliorate the severe environmental impact of palm oil, both compositionally and functionally, have so far failed to effectively conserve biodiversity (Edwards et al., 2010; Edwards et al., 2013). It would therefore be interesting to assess, if networks of isolated *Ficus* trees survive or have established themselves in palm oil plantations (as they have done in Assamese tea estates), whether they can enhance environmental conditions within palm oil plantations, while only occupying small areas of land, as they do in tea estates in Assam. If *Ficus* trees do persist in palm oil plantations, and if the survey methods of Chapters 4 and 5 could be replicated, the results may provide a much-needed stimulus to human-modified landscape conservation policy in South-east Asia.

Three other areas would benefit from further analyses of *Ficus*–frugivore dynamics in human-modified landscapes. First, this thesis focused on a particular subset of *Ficus* species, unified by their large, hemi-epiphytic or free-standing tree growth forms. It would therefore be interesting to build on these results, and investigate ecological relationships between smaller *Ficus* species and frugivores in similar human-modified landscapes. Although they do not produce fruit on the same scale as the larger species, *Ficus* vines, epiphytes, and shrubs share several other fruit characteristics, including phenology, nutrient content, and ease-of-handling. Indeed in Singapore, Metcalfe et al. (1998) found the shrubs *F. grossularioides* and *F. chartacea* can

produce ripe fruit at 0.4 m and 2 m height, respectively, and provide fruit throughout the year. The potential importance of smaller *Ficus* species to avian frugivores was highlighted by Breitwisch's observation of birds feeding at a *Ficus* vine in Cameroon (Breitwisch, 1983). Over an eight-day period, he estimated that three greenbul (Pycnonotidae) species consumed a total of 17,000 fruits, with 4,700 consumed by fruit pigeons, and 2,500 by hornbills. These smaller *Ficus* species may not commonly attract large flocks of wide-ranging frugivorous birds, but they may still play an important role supporting communities of locally distributed frugivores, such as the bulbuls, treepies, and some of the mynas recorded in this study. Additional work investigating the relationship between these *Ficus* growth forms and frugivores in human-modified landscapes may also uncover some interesting dependencies, especially if smaller *Ficus* species were compared to other non-*Ficus* vines, epiphytes, and shrubs.

A wider geographical scope would also provide an interesting lens through which to view the results of this thesis, and to address some long-standing debates within *Ficus*–frugivore ecology. For example, although a strong link between *Ficus* trees and frugivores has been reported in numerous cases where tropical frugivory has been studied (Shanahan et al., 2001), there is some doubt over the extent to which *Ficus* trees provide an important fruit resource in West Africa (Gautier-Hion & Michaloud, 1989).

Additionally, although a considerable amount of work has been conducted into conservation in human-modified landscapes in Central America, a comparative study, which assessed the importance of *Ficus* trees for frugivorous birds relative to other common isolated trees (see for example Luck & Daily's 2003 study of frugivorous birds and isolated *Miconia* trees in Costa Rica) is still lacking. The results of such a

study would be particularly interesting to contrast with those of this thesis, as it may also bring into focus the differing religious values attributed to *Ficus* trees, and whether this has any broad effect on their suitability as micro-sites for conservation in human-modified landscapes.

CHAPTER 13: CONCLUSION

This thesis sought to assess potential conservation strategies in tropical and subtropical human-modified landscapes. By studying isolated *Ficus* trees in Assam, North-east India, three emergent themes concerning conservation beyond protected areas were addressed: biodiversity conservation per se, restoration ecology, and human–environment relationships.

Turning to biodiversity conservation first, isolated *Ficus* trees, when compared to other common isolated trees in a human-modified landscape, had higher species richness and abundance of frugivorous birds. In a completely novel finding, isolated *Ficus* trees were also important for insectivorous birds, a group that is particularly vulnerable to habitat modification. This is the first comparative study to verify the importance of *Ficus* trees to these two foraging guilds beyond the forest edge, and the particularly high numbers of frugivorous birds visiting isolated *Ficus* trees suggests that the conservation of these trees may yield disproportionate conservation returns. Furthermore, in the first analysis of bird functional diversity at the scale of individual trees, maximum gape size and the functional dispersion index were fairly robust to increasing isolation, so that even *Ficus* trees located at distances of over 30 km were visited by birds that represented the majority of functional space in the overall assemblage. Given that these functional dispersion scores were significantly higher in *Ficus* trees than non-*Ficus* trees, it appears possible to conclude that isolated *Ficus* trees may be more useful in conserving functional traits of bird assemblages in human-modified landscapes than other tree types.

Considering the higher abundance and diversity of frugivores visiting isolated *Ficus* trees, it is perhaps unsurprising that the richness and abundance of saplings growing under *Ficus* trees, compared to non-*Ficus* trees, was also higher. This result helps to

inform the second key theme: restoration ecology. The extent of deforestation across the tropics, and subsequent land abandonment in many areas, means that identifying affordable, expeditious, and ecologically appropriate methods of restoring forest is an increasingly high conservation priority. Within this framework, methods such as mixed native plantations and applied nucleation have their own advantages and disadvantages, but where *Ficus* trees are present, they may offer the best overall solution in terms of cost, speed, and assemblage representativeness. If conservation strategies that encouraged landowners to reduce grazing pressure around isolated *Ficus* trees were initiated successfully, it may be possible to enhance forest restoration at little to no cost. Furthermore, our results indicated that the plants growing under *Ficus* trees had numerous beneficial applications as goods and medicinal products for the locals in rural Assam, and that isolated *Ficus* trees provided such goods at significantly higher densities than other isolated trees. Therefore, the conservation of isolated *Ficus* trees offers the prospect of delivering dual ecological and humanitarian benefits in human-modified landscapes.

Building upon the provision of important local plant resources, *Ficus* trees have a long and somewhat complex history of eminence in human societies in Assam and beyond. The holy status of *F. religiosa* and *F. benghalensis* in Hinduism and Buddhism was reflected in numerous reports of their sacredness, and taboos on felling *Ficus* trees in the study area. However, several observations of figs being cut down, and further ethnographic enquiries revealed a more practical relationship between humans, faith, and *Ficus*. Despite their religious properties, the economic costs imposed by the shade and extensive roots of *Ficus* trees meant that they were subject to clearance in agricultural areas, and the roadside growing locations of the majority of *Ficus* trees in the study area meant that they were vulnerable to road expansion

programmes. A more practical attitude towards *Ficus* than might otherwise be assumed was also apparent in the results of the global *Ficus* social survey. The survey not only confirmed that the religious attributes of *Ficus* trees were subject to substantial geographical variation, but also found that the highest reported felling rates were also in the regions where *Ficus* trees recorded the highest scores for religious value. Despite the increasingly vocal calls for religious or spiritual beliefs to be invoked in promoting the conservation of sacred sites, the results of the ethnographic fieldwork and global survey imply that positioning *Ficus* trees as micro-scale sacred natural sites may be less successful than emphasising some of their other intangible and utilitarian benefits, such as their aesthetic beauty and the provision of shade for shelter.

Looking forward, population simulation models for the two most common *Ficus* species in the study area, *F. religiosa* and *F. benghalensis*, projected that *Ficus* trees are likely to increase in density in the study area over the next 300 years. However, both species were very sensitive to increases in adult mortality in the models. Given the important role isolated *Ficus* trees have been demonstrated to play in avifaunal conservation, both compositionally and functionally, as well as their efficacy in assisting vegetation regeneration, and their significant socio-economic position, it would be prudent to instigate measures to ensure the survival of isolated *Ficus* trees in this human-modified landscape and in other similar environments where *Ficus* trees currently persist.

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APPENDIX 1:

The keystone species concept: a critical appraisal

A1.1 Preface

While conducting background research into previous studies of *Ficus*, it became apparent that almost all authors referred to *Ficus* trees as ecological keystones. As these studies were predominantly from forest habitats, it raised the question: are *Ficus* trees still keystones in human-modified landscapes? However, on examining the definition of an ecological keystone, and evaluating methods to test for the existence of keystones, it soon became clear that no satisfactory definition or test had been developed. This thesis therefore avoids referring to *Ficus* as keystones, but instead outlines the shortcomings in the keystones field with the following review of the literature.

Authors: H. Eden W. Cottee-Jones & Robert J. Whittaker

The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the literature review: HEWC-J. Wrote the paper: HEWC-J, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

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A1.2 Abstract

The keystone concept has been widely applied in the ecological literature since the idea was introduced in 1969. While it has been useful in framing biodiversity research and garnering support in conservation policy circles, the terminology surrounding the concept has been expanded to the extent that there is considerable confusion over what exactly a keystone species is. Several authors have argued that the term is too broadly applied, while others have pointed out the technical and theoretical limitations of the concept. Here, we chart the history of the keystone concept's evolution and summarise the plethora of different terms and definitions currently in use. In reviewing these terms, we also analyse the value of the keystone concept and highlight some promising areas of recent work.

Keywords community composition, ecosystem engineer, definitions, dominant species, keystone concept, keystone species

A1.3 Introduction: the origins of the concept

The keystone concept has its roots in food-web ecology, and was coined by Paine (1969). In his experimental manipulation of rocky shoreline communities on the Pacific coast in Washington, Paine found that the removal of the carnivorous starfish *Pisaster ochraceus*, the top predator of the local system, led to the local extinctions of several benthic invertebrates and algae (Paine, 1966). In a subsequent short note (Paine, 1969:92) he used this example, alongside that of the impact of another starfish *Acanthaster planci*, on parts of the Great Barrier Reef, to argue that “the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community’s structure, and the integrity of the community and its unaltered persistence through time, that is, stability, are determined by their activities and abundance. They may be unimportant as energy transformers.” He argued, in effect, that the keystone species had a disproportionate influence on key community properties and explicitly claimed that variation in the abundance of other predators “would produce no impact comparable to that produced by variations in the keystone species” (p. 93). Paine’s field experiments have become a classic ecological case study, with his diagrams reproduced in many standard ecology texts, his 1966 paper cited 2,509 times, and his note coining the term “keystone species” 465 times (ISI Web of Knowledge 13th September 2012). The concept itself has become widely used, with over 1,600 articles using it in their title or to describe their topic (ISI Web of Knowledge 13th September 2012).

Throughout the 1970s and 1980s a range of species were identified as keystone species. In marine ecosystems the sea otter (*Enhydra lutris*) was found to control sea urchin populations along the Aleutian Islands, which maintained littoral and sub-littoral community structure and increased species diversity and primary productivity (Estes & Palmisano, 1974). In freshwater ecosystems in North America, beavers (*Castor canadensis*) were found to

influence plant and animal community composition and richness in wetland and riparian habitats (Naiman et al., 1986), while in terrestrial ecosystems pocket gophers (Geomyidae) were believed to keep North American prairie soils in a condition that could support higher plant diversity (Huntly & Inouye, 1988). The concept was also applied palaeoecologically, with North American megafauna described as “keystone herbivores” that created a mosaic of open woodlands and grasslands during the Pleistocene (Owen-Smith, 1987). In policy dialogues the keystone concept was championed by Simberloff (1998), because managing keystone populations was thought to help conserve the populations of other species in protected areas (Carroll, 1992; Caro, 2010).

A1.4 Expansion of the keystone concept

While Paine originally intended keystone species to refer to those species that maintained the stability of an ecosystem (like the keystone in an arch), this idea was not retained in the subsequent development of the term. In fact, his reference towards a disproportional relationship between the keystone species and the community was lost in some reconfigurations, while others abandoned the notion of a single species being the keystone. For example, Gilbert (1980) proposed that plants which provide critical support to complexes of pollinators and dispersers should be described as keystone mutualists, which if lost from an ecosystem would lead to a collapse in functionality and species richness. The idea of ecological collapse was then developed by Terborgh (1986), who argued that, in Neotropical forest ecosystems at least, a handful of keystone plant resources were critical to providing food for frugivores during the fruit-scarce dry season, and so set the carrying capacity of the community. He suggested that a reduction in frugivore populations would follow the removal of such keystone plant resources, and the subsequent loss of seed-dispersal pathways in the forest would result in a decrease in species richness through a cascade of extinctions.

While the keystone concept became popular in both research and policy arenas, it was not without its critics. For example, Mills et al. (1993:219) argued that the term was “broadly applied” and “poorly defined” and that basing conservation strategies on keystone species was dangerous. Indeed the evolution of terminological confusion, which Peters (1988) described for food-web ecology, could just as easily be applied to the keystone concept (see Figure A1.1).

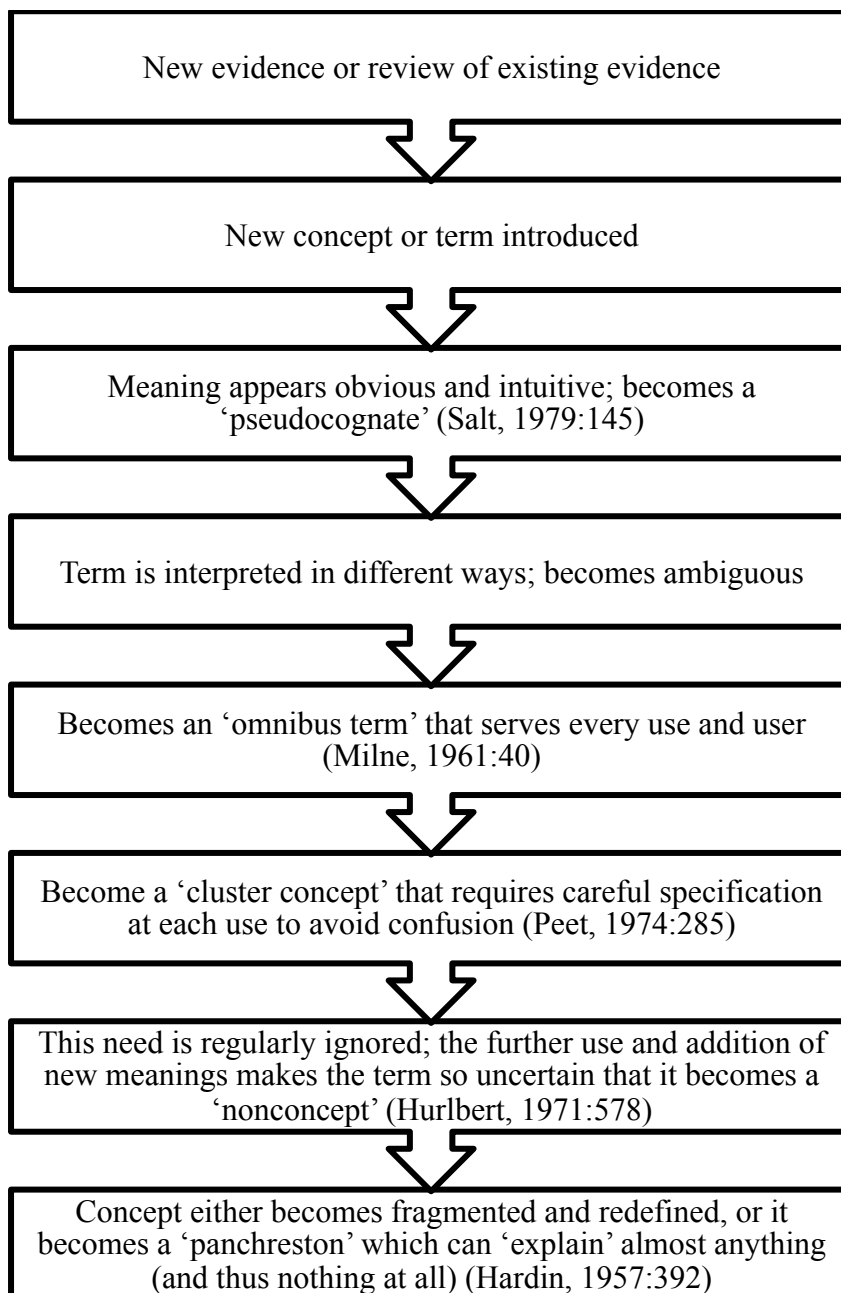


Figure A1.1: The demise of a scientific term (following Peters, 1988).

In response to the challenge of identifying keystone species more precisely, a small conference was held in Hilo, Hawaii (8–11 December 1994), where international policy practitioners and ecologists who had worked on the keystone concept attempted to produce a consensus definition of a keystone species. They agreed on the following definition: “a keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance” (Power & Mills, 1995:184) and published a paper the following year where they attempted to identify the magnitude of the influence one species has on its community, known as its “community importance” (Power et al., 1996).

Despite this attempt to pin down a definition of keystone species and produce a tool to identify species that fit the consensus definition, confusion still surrounds the term (Piraino & Fanelli, 1999; Barua, 2011). This may be because: 1) the definition from Hilo retains a large degree of ambiguity; and 2) the community importance tool remains incomplete, with no quantitative threshold to determine the level of community importance needed to gain keystone status. Nonetheless, researchers continue to apply the concept to an ever-growing number of species and scenarios. For example, in 2010 and 2011 the Nile Crocodile (*Crocodylus niloticus*), Black Woodpecker (*Dryocopus martius*), European Rabbit (*Oryctolagus cuniculus*), Plateau Pika (*Ochotona curzoniae*), a parasitic fungus (*Ophiocordyceps unilateralis*), a species of Japanese bamboo grass (*Sasamorpha borealis*), the Brown Bear (*Ursus arctos*), Grey Wolf (*Canis lupus*), Eurasian Lynx (*Lynx lynx*), Black-tailed Prairie Dog (*Cynomys ludovicianus*), Bearded Goby (*Taenioides jacksoni*) and a squid (*Loligo plei*) were all described as keystone species (Ashton, 2010; Gasalla et al., 2010; Konsinski et al., 2010; Moloney, 2010; Delibes-Mateos et al., 2011; Evans et al., 2011; Magle & Angeloni, 2011; Tsuyama et al., 2011; Ucarli, 2011). While the high number of species identified as keystones does not mean they are inaccurate, different definitions are

being applied, resulting in a lack of consistency in the criteria used to assign keystone status. For example, the European Rabbit was awarded keystone status because of the disproportionate effect it has on community function relative to abundance (Delibes-Mateos et al., 2011), while the Bearded Goby was given keystone status because it plays a “unique ecological role” on the Namibian continental shelf (Moloney, 2010:5). This list further reflects the three main problems with the definition of keystone species, namely: 1) there are too many alternative definitions in the literature; 2) the definitions are often vague and imprecise; and 3) the term has been expanded to encompass a range of other ecological relationships (Tables A1.1 and A1.2).

Table A1.1: A selection of published definitions for the term “keystone species”.

Keystone species definitions (adapted)	Reference
Definitions involving a strong influence	
A species whose population is “the keystone of the community’s structure”, whereby the integrity and stability of the community are determined by its activities and abundance.	Paine, 1969:92
“Keystone species are those whose removal from a community would precipitate a further reduction in species diversity or produce other significant changes in community structure and dynamics.”	Daily et al., 1993:592
“Keystone species play a critical role in determining community structure.”	Jones et al., 1994:380
“Relatively rare species in a community whose removal causes a large shift in the structure of the community and the extinction of some species.”	Krebs, 2009:378
“Rare species of low abundance in a community but whose removal has drastic effects on many other species in the community.”	Krebs, 2009:402
Definitions involving a disproportionate effect relative to abundance	
Species which “have a disproportionate effect on the persistence of all other species.”	Bond, 1993:236
“A species whose impacts on its community or ecosystem are large and greater than would be expected from its relative abundance.”	Heywood, 1995:290
A species “whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance.”	Power et al., 1996:609
“Consumers having a disproportionately large effect on communities and ecosystems.”	Menge & Freidenburg, 2001:622
Definitions involving a disproportionate effect relative to biomass	
A species which has “impacts on many others, often far beyond what might have been expected from a consideration of their biomass or abundance.”	Simberloff, 1998:254
“A species that has a disproportionate effect on its environment relative to its biomass. Such organisms typically have a strong influence on many other organisms within an ecosystem and may play an important role in determining the structure of the ecological community.”	Ladle & Whittaker, 2011:261

The extension of the keystone term to include other elements, such as mutualisms, guilds, etc., further complicates the task of delimiting the meaning of the term (Table A1.2). If these tables make one thing clear, it is that the number and range of keystone concept definitions has reached unworkable levels, and is in need of refinement. There are two options here: 1) formulate a specific definition of “keystone”, with testable quantitative thresholds, which would allow researchers to discard or include the wealth of species currently listed as keystones; or 2) use a general definition that encompasses the current interpretation of the keystone concept, which can be broadly applied, and which has no quantifiable thresholds or criteria. The first option is preferable, but for reasons discussed below, there are larger theoretical and practical issues that constrain the validity of the keystone concept. Therefore it may be sensible to follow the second option, and propose a general definition that reflects the current use of the keystone idea in scientific, policy, and public settings. So in practice, by reference to the way that the term is used in much of the literature, it would be more defensible to describe the current usage as follows: “a keystone species is a species that is of demonstrable importance for ecosystem function”. For the variants of the keystone concept, the word species is substituted with the relevant term (for example a keystone structure would be a structure that is of demonstrable importance for ecosystem function). This abandons the notion of proportion that existed in earlier definitions, and moves away from the original idea of ecosystem stability. It also gives practitioners and the public a common reference point which conveys the central message it is believed to carry, and perhaps more importantly, it does not give any false illusions of being a precise scientific term.

Table A1.2: Other variants of the keystone concept and their definitions.

Term	Adapted definition	Example	Reference
Keystone Mutualist	“[T]hose organisms, typically plants, which provide critical support to large complexes of mobile links.” (Where mobile links are animals required by many plants for reproduction and dispersal).	The canopy tree <i>Casearia corymbosa</i> (Howe, 1977)	Gilbert, 1980:32
Keystone Plant Resource	Those plants which play “prominent roles in sustaining frugivores through periods of general food scarcity.”	<i>Ficus</i> trees, palm nuts	Terborgh, 1986:339
Extended Keystone Hypothesis	“All terrestrial ecosystems are controlled and organized by a small set of key plant, animal, and abiotic processes.”	North American forest insect pests (Holling, 1986)	Holling, 1992:449
Keystone Modifier	Those “species which greatly affect habitat features without necessarily having direct trophic effects on other species.”	North American Beaver <i>Castor canadensis</i> (Naiman et al., 1986)	Mills et al., 1993:220
Keystone Guild	Where similar species in an ecosystem are “known to have impacts that are disproportionally large relative to their collective biomass.”	Flying foxes (<i>Pteropus</i> spp.) on Samoa (Elmqvist et al., 1992)	Power et al., 1996:613
Reverse Keystone Species	A species which “must be absent or at very low density if a typical species-rich assemblage...is to be sustained in a local area.”	Noisy Miner (<i>Manorina melanocephala</i>)	Piper & Catterall, 2003:609
Cultural Keystone Species	“Those plant and animal species whose existence and symbolic value are essential to the stability of a culture over time.”	Cocoa in various indigenous Amazonian communities	Cristancho & Vinning, 2004:153
Keystone Structure	Ecological structures which “exert a disproportionate effect on ecosystem function in a wide range of ecosystems”, the loss of which “may lead to the deterioration of important ecosystem functions.”	Dehasas scattered tree landscapes in Spain and Portugal (Díaz et al., 1997)	Manning et al., 2006:311; Tews et al., 2004

A1.5 Theoretical and practical constraints to providing a precise definition of

“keystone”

The idea of proportionality, where a keystone species had to have a disproportionate influence on its community relative to either its abundance or biomass, introduced a great deal of uncertainty into the concept, without necessarily being well grounded biologically (Mills et al., 1993). In order to identify a keystone species, it meant that all the individuals of all species in a community had to be counted, or that the biomass of the suspected keystone species had to be compared in relative terms to the biomass of the entire community. While

both conditions are extremely difficult to satisfy in practice, the vast majority of species are likely to have a very small biomass relative to their entire community, and so with this clause most species, and almost every top predator, could be described as a keystone species.

While this attempted re-definition may just confirm that the keystone concept has become a panchreston, where it is so vague that it can “explain” almost anything (Hardin, 1957:392), it at least avoids the complications of proposing a more quantifiable, precise definition – which is difficult to defend because such implementations of the keystone concept are almost impossible to test. This general definition also avoids the debate over whether keystone species should maintain species richness, community structure, productivity or nutrient cycling pathways, by emphasising ecosystem function instead. This updates keystone theory from its original reference to ecosystem stability, which lacks empirical support in many natural or semi-natural systems. Instead, a focus on ecosystem processes aligns the keystone concept with biodiversity conservation and the idea of functional resilience, defined as the amount of disturbance an ecosystem can withstand “without changing self-organised processes and structures” (Gunderson, 2000:425).

Returning to the genesis of the concept, in Paine’s (1966) study the scientific basis for his claim was rather limited, which leads one to question the validity of *Pisaster ochraceus* as a keystone species, even in the terms of the original definition. Paine’s field site was an eight metre-long fragment of shoreline in Mukkaw Bay, Washington State, and the only species removed from the experimental area was *P. ochraceus*. There were no neighbouring experiments where other species were excluded and there was no replication. Rather, Paine (1969:92) wrote that “indirect evidence strongly suggests that equivalent changes do not appear with the exclusion of other consumers”. Furthermore, when Menge and colleagues conducted experiments on other areas of the Pacific coast in Oregon, they found that *P.*

ochraceus only played an important role in wave-exposed sites, and so this particular starfish did not merit keystone status more generally across space (Menge et al., 1994).

The second case study Paine used as evidence for the existence of keystones was from the Great Barrier Reef, Australia. In the 1960s the population of the starfish *Acanthaster planci* reached plague proportions, and was destroying large sections of the reef by feeding on hard corals. At the time, tritons of the *Charonia* genus, which prey on *A. planci*, were being over-exploited by the tourist souvenir industry, and so Paine hypothesised that *Charonia* had been acting as a keystone, holding densities of *A. planci* at low levels and thus preserving a diversity of hard corals. However, *Charonia* snails can only eat about one *A. planci* per week, and so their capacity to control the starfish's population appears limited. Furthermore, the sites of the initial 1962 outbreak did not correspond with the sites that were most visited by tourists; and following their protection in 1969, triton snails are no longer collected, yet there were subsequent outbreaks of *A. planci* in 1979, 1994 and 2003. Instead the fluctuations in *A. planci* populations are believed to be the result of a combination of factors, involving other predators such as the Humphead Maori Wrasse (*Cheilinus undulates*) and human influences on the Great Barrier Reef's water quality, where coastal run-off has increased nutrient levels, improving survival rates of *A. planci* larvae (Harriott et al., 2003). The evidence that *A. planci* outbreaks were mediated by the exploitation of a hypothetical keystone in *Charonia* snails was anecdotal in 1969 (Bond, 1993), and in light of later work it appears that Paine's assumptions may have been unjustified.

Subsequent attempts to identify keystone species have fallen foul of similar methodological criticisms and overt subjectivity (Mills et al., 1993; Hurlbert, 1997), leading to several attempts to formulate a standardised methodology to identify "keystones". Power and colleagues divided possible methods into two categories: experimental and comparative (Power et al., 1996). Experimental techniques follow Paine (1966) and involve the exclusion

of suspected keystone species from the community. To be thorough, this method should be followed for all species in the community, which leads to logistical difficulties on top of the ethical issues surrounding such experimental manipulation. Further issues over scale effects, both spatially and temporally, ought to be considered, especially given that the demands of excluding species often means that the study site has to be small (Menge et al., 1994; Power et al., 1996; Wootton, 1997). The second method, comparative studies, involves comparing two sites with different densities or presence/absence of potential keystone species. Drawing robust conclusions from such analyses is often difficult, however, because confounding factors may mask ecological relationships (Gotelli et al., 2011).

A1.6 Testing for “keystones”

While there are problems with both of these methods, there are greater issues in assessing the strength of interactions between a potential keystone and other species in the community. Power and colleagues built on Paine’s (1992) “interaction strength” in developing their community importance index, which measures “the change in a community or ecosystem trait per unit change in the abundance of the species” (Power et al., 1996:609). Their method relied on the experimental approach because of the difficulty in measuring the effects of small changes in abundance, and unlike Paine, who used a per capita measure, Power and colleagues normalised a species’ impact by using its proportional biomass. In a recent contribution, which reverts to the per capita approach, Novak and Wootton (2010) developed Paine’s 1992 index and Wootton’s (1997) dynamic index. In order to scale out differences in population size, they defined the per capita interaction strength between species as the “direct effect that one individual of the first species has on one individual of the second species per unit time” (Novak & Wootton, 2010:1057). While they argued that the appropriate experimental interaction strength index is the correct way to test species interactions, they

admitted that each index is subject to several assumptions, which often leave empirical ecologists frustrated with theory that cannot readily be applied to natural systems.

In an attempt to avoid the problems of experimental manipulation, Gotelli et al. (2011) employed a comparative statistical methodology that analysed ecological variables in unmanipulated samples. Their method uses randomisation tests to quantify the average effect a particular species' presence or absence within these samples has on a set of ecological variables. In contrast to Power et al. (1996), they avoided scaling their results by abundance or biomass because the measures for rare species would be divided by a small number, greatly inflating the uncertainty and errors in the index (Gotelli et al., 2011:640). While this procedure worked for biological crust communities in central Spain, they found that estimates of species importance were still confounded by particularly strong species interactions, unmeasured abiotic variables, and the reciprocal effects of environmental variables on species presence (Gotelli et al., 2011:634).

Novel approaches to identifying community importance or interaction strength include measuring the unique ecological function that cannot be provided by a different species (Perry, 2010), community viability analyses (Ebenman & Jonsson, 2005), community sensitivity analyses (Berg et al., 2011) and network analyses (Jordán, 2009; Aizen et al., 2012; Lewinsohn & Cagnolo, 2012; Pocock et al., 2012). Further exploration of these avenues may offer ways to rank, on a quantitative basis, the importance of a species to a community, and therefore identify a threshold for keystone species, but all have significant obstacles to overcome. Network and sensitivity analyses, for example, rely on simplifying complex ecological relationships, and excluding some effects so that the network size is small enough to analyse. However, aggregating species into groups will lead to inaccuracies, and isolating parts of ecological networks will exclude potentially important external effects (Jordán, 2009). These new approaches also still struggle with context dependency in the

identification of keystone species, i.e. where a species can be a keystone in one community but not in another very similar community, either across space or over time (Mills et al., 1993; Menge et al., 1994; Christianou & Ebenman, 2005). This point has been illustrated in the range of results found in recent network studies, where plants, higher taxonomic families, and interactions rather than organisms were the keystone components in the organisation of three communities (Aizen et al., 2012; Lewinsohn & Cagnolo, 2012; Pocock et al., 2012; Stouffer et al., 2012). Until a satisfactory method can be found to determine a threshold for keystone species delimitation, a precise scientific definition will remain elusive.

A1.7 Alternatives to the keystone concept

The keystone concept is also plagued by issues beyond its own definition and the quantitative identification of keystones. Further terminological confusion is introduced by the overlap of the keystone concept with other terms, such as “ecological dominant”, “ecosystem engineer” (which is used interchangeably with “ecological engineer”), and “foundation species” (Table A1.3). This has led to the misapplication of each of these terms, as discussed below.

Table A1.3: Competing terms close to keystone species in meaning.

Term	Adapted definition	Example	Reference
Dominant Species	“The abundant and controlling species of characteristic life-form were long ago termed dominants (Clements, 1907; 1916), this property being chiefly determined by the degree of reaction and effective competition.”	Shrubs in chaparral and desert ecosystems	Clements, 1936:270
Ecological Engineer	“organisms that directly or indirectly modulate the availability of resources to other species, causing physical state changes in biotic or abiotic materials.”	North American Beaver <i>Castor canadensis</i> (Naiman et al., 1986)	Jones et al., 1994:373
Foundation Species	“are disproportionately important to the continued maintenance of the existent community structure.”	<i>Hedophyllum sessile</i> , <i>Strongylocentrotus purpuratus</i> , <i>Pycnopodia helianthoides</i>	Dayton, 1972:86

The close links between the “dominant species” concept and the “keystone species” concept provide a good example of two terms that can easily become confused. Indeed, we contend that the distinction between the terms is unclear and unresolved and that this owes much to the fact that the two terms originated in different branches of ecology at points separated by around half a century: the dominant species being a product of early 20th century phytosociology and the keystone species being conceived initially by a zoologist examining food-web structures. The plant ecologist F.E. Clements was writing on the role of the dominant around 100 years ago (see Table A1.3). In short, within his view of the community as a super-organism, the dominants were the species of greatest biomass, which shaped the character of the community and which were diagnostic to the community identity. They were, moreover, crucial to the maintenance of the steady state of the climax community, just as Paine (1969) represented the keystone species as crucial to the stability of the shoreline food web. The distinction between the two concepts thus appears to mostly reflect the notion that a keystone species has an influence in some way disproportionate to its abundance: a notion integral to most definitions of the keystone concept (Table A1.1), but one which appears hard to empirically test (above). In practice, a species may be both keystone and dominant, or it may in theory be one without quite being the other, assuming we can find a means to distinguish between proportionate and disproportionate degrees of influence and assuming that we can agree on whether the maintenance of stability is integral to one or both concepts.

A second area of overlap exists between keystone species and ecosystem engineers. Ecological engineers have been defined as “organisms that directly or indirectly modulate the availability of resources to other species, causing physical state changes in biotic or abiotic materials” (Jones et al., 1994:373). Examples include the North American Beaver (*Castor canadensis*), prairie dogs (*Cynomys* spp.) and the African Elephant (*Loxodonta africana*) (Naiman, 1988; Whicker & Detling, 1988). As this list suggests, many species described as

ecosystem engineers have also been described as keystone species, and it is unclear whether engineers have in fact been mislabelled as keystones. For example, while the Red-naped Sapsucker (*Sphyrapicus nuchalis*) has been described as a keystone species because of its habit of excavating nest holes that are used by a range of secondary cavity-nesting birds (Daily et al., 1993), this behaviour is better described as ecological engineering. It appears that misclassification may be a problem, a concern compounded by recent definitions of ecosystem engineers that have also introduced the idea that engineers provide ecological stability, much as keystones were originally argued to do (Dudgeon & Petraitis, 2005). The overlap between the two concepts is also highlighted by the parallels between ecological engineers and “keystone modifiers” (Lawton & Jones, 1995). Keystone modifiers are defined as species which greatly affect habitat features without necessarily having direct trophic effects on other species (Mills et al., 1993). Caro (2010:144) argued that ecosystem engineers differ from keystone species in that they can act in concert, whereas keystones are always individual species, and because engineers alter their physical environments, whereas keystones influence their communities. While many supposed keystones are individual species, keystone mutualists act in concert in the same way ecosystem engineers are believed to act, and as outlined above, keystone modifiers can change their environment as well as their community. Caro (2010) did admit, however, that ecosystem engineers should be considered to be a subset of keystone species, and Power et al. (1996) argued that the two terms are interchangeable, therefore subsuming all engineers within the keystone concept.

An even more difficult distinction is between keystone and foundation species. Dayton’s (1972) definition of foundation species (see Table A1.3) overlaps with both the dominant and keystone species concepts. Indeed the limited uptake of the term ‘foundation species’ in the literature suggests that it has been subsumed within the keystone concept, which is intriguing given that both Paine and Dayton were working in the same intertidal habitats in Mukkaw

Bay at the time, and had described them as separate concepts (Paine, 1969; Dayton, 1971; 1972).

Recent research has introduced more confusion. Ellison and colleagues defined a foundation species as one which “controls population and community dynamics and modulates ecosystem processes”, and differentiated between foundation species and keystone species: keystones “...are usually top predators” and foundation species “usually occupy lower trophic levels” (Ellison et al., 2005:479). Furthermore, according to Ellison et al. (2005), the fifth class of Jones and colleagues’ typology of ecological engineers, the “autogenic ecosystem engineer” (Jones et al., 1994), is directly analogous to Dayton’s (1972) foundation species. It is thus evident that there are a number of alternative ways in which the same community relationships can be defined, as well as a lack of clear separation between terms as they are used by different authors and in different sub-fields of ecology.

A1.8 Conclusion

Although there are many more terms that overlap with the keystone concept, extricating all their exact definitions is beyond the scope of this paper. Indeed, figuring out the meaning of the keystone concept itself has turned out to be challenging enough. Although Paine may have originally meant for the keystone concept to be a metaphor (Paine 1995), it has been used as a scientific term for decades – despite the failed attempts to improve the precision and consistency of its use. Indeed, given the difficulties of providing a standard quantitative test to identify keystones, especially considering the context dependency of species’ community importance and the practical problems with existing field methodologies, there appears to be little prospect of developing a robust definition with the required thresholds or criteria. We propose a definition that, if accepted, may provide a consistent reference point and simplify the confusion surrounding the term: “a keystone species is a species that is of demonstrable importance for ecosystem function”. In the meantime, the list of species labelled as keystones

will continue to grow. We see some danger in this because the agency the term has with policy makers and the public appears to owe more to the imagery of the keystone analogy than to scientific validation that particular species, guilds, or groups justify the use of the term in an objective sense. Perhaps, in the end, this is the real value of the term – not so much an operational scientific concept, but rather a metaphor, and one which allows scientists to convey swiftly and powerfully an image of the interdependency of living things, and of the potential for seemingly unimportant species to have, in practice, a really important functional role that merits conservation action (Barua, 2011)?

A1.9 Acknowledgements

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A1.10 References

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APPENDIX 2:

The persistence of the *Ficus*–frugivore relationship beyond protected areas

A2.1 Preface

This thesis built upon the findings of an undergraduate dissertation investigating preliminary questions in part of the same study area, conducted in May–August 2009. The field data collection method differed slightly, with 30-minute bird surveys rather than three-hour surveys, but the results helped shape the ideas and questions for this larger study of the same system. The following appendix presents a summary of these earlier results, in which the undergraduate data were reanalyzed during the first year of the DPhil, which explore some aspects of the system that the DPhil does not consider.

Authors: H. Eden W. Cottee-Jones & Robert J. Whittaker

The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J. Analysed the data: HEWC-J. Wrote the paper: HEWC-J, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This appendix was submitted to *Tropical Ecology* on 24/05/2012, and after revision, it is undergoing a second round of peer-review.

A2.2 Abstract

Conservation beyond protected areas is increasingly recognised as an important strategy for tropical regions, especially in deforested areas. However, the extent to which mutualistic relationships are maintained beyond the forest edge is poorly understood, even for functionally important species groups. Here, we seek to identify the persistence of a critical plant–frugivore relationship by studying the bird assemblages feeding on *Ficus* trees scattered beyond protected areas in a tropical countryside landscape in Assam, India. We surveyed 53 fruiting *Ficus* trees, recording 76 bird species, 31 of which were frugivores. We found evidence for resource partitioning, whereby birds selectively favoured *Ficus* species with small, bright, odourless fruit, within these ‘countryside’ landscapes. Scattered *Ficus* trees were also found to be important food resources for migratory frugivores, with flocks of up to 385 Spot-winged Starlings visiting individual *Ficus* trees in a 30-minute period. Finally, we found no evidence that the classic predictors of assemblage composition beyond protected areas – distance and disturbance – had an effect on frugivore abundances in scattered *Ficus* trees. Our results suggest these species are tolerant of tropical countryside landscapes, and that the mutualistic relationship between *Ficus* trees and avian frugivores may be capable of persisting outside protected areas.

Keywords Assam, birds, conservation, *Ficus*, India, scattered trees, seed dispersal, tropical countryside biogeography

A2.3 Introduction

Habitat loss and fragmentation are major drivers of biodiversity loss in the tropics (Lindenmayer & Fischer, 2006; Gibson et al., 2011). Although conservation efforts have traditionally focused on conserving species through protected areas, there is a growing recognition of the effectiveness of conservation measures in human-modified landscapes beyond protected areas (Franklin & Lindenmayer, 2009; Gardner et al., 2009; Wright et al., 2012). The long-term viability of conservation strategies, within and beyond protected areas, at least partially depends on the persistence of ecological functions such as pollination, nutrient cycling, and seed dispersal (McConkey et al., 2012). Seed dispersal, for example, is critical to seedling survival in many species, and helps determine species compositions and abundances across the world's tropical forests (Howe & Miriti, 2000). For many plants, seeds are dispersed through interactions with frugivorous birds and mammals (Harrison et al., 2012). However, these interactions are vulnerable to collapse in landscapes beyond protected areas, where habitat conditions may not suit the dispersal agents (Vidal et al., 2013). Important determinants of frugivore presence in modified landscapes are believed to be the distance from the nearest protected area or forest, and the level of human disturbance (Eshiamwata et al., 2006; Kirika et al., 2008; Herrera & Garcia, 2009).

Ficus trees are a critical food resource for frugivores across the world's tropical forests, with over 1,200 tropical birds and mammals recorded feeding on their fruit (Shanahan et al., 2001). In Assam, India, several *Ficus* species survive in modified landscapes, presenting an opportunity to study the condition of this important plant–frugivore relationship beyond protected areas. These *Ficus* species can be divided into two groups based on their fruit presentation and primary dispersal agents. Bird-dispersed *Ficus* have fruit that is odourless, bright, and small (approximately 8 mm in diameter), and which are primarily handled by birds, whereas predominantly mammal-dispersed *Ficus* species have odorous, dull, and large

fruit (approximately 20 mm in diameter) (Van der Pijl, 1982; Gautier-Hion et al., 1985). Although this division of resources has been identified in intact forests (Lambert & Marshall, 1991; but see Harrison et al., 2012), little is known about the fidelity of each dispersal group to fruit presentation in modified landscapes, where there may be fewer opportunities for frugivory.

We sought to examine the state of plant–frugivore relationships beyond protected areas by studying scattered *Ficus* trees in Assam, India. In particular, we wanted to discover whether: 1) the division between bird- and mammal- dispersed *Ficus* fruit is maintained beyond protected areas; 2) land-use intensity or distance had an effect on bird visitation at scattered *Ficus* trees; and 3) disturbance-tolerant species were dominant within the major *Ficus* avian frugivore guilds: pigeons, barbets, starlings, and mynas.

A2.4 Methods

A2.4.1 Study area

The study was conducted in the human modified landscape of Kaziranga District, Upper Assam, India (26.586762, 93.429537). Kaziranga had sub-tropical deciduous forests until the mid-nineteenth century, when most of the local forests were cleared following the commercialisation of tea production, with the exception of the 430 km² Kaziranga National Park and 7.65 km² Panbari Forest Reserve. The landscape beyond these protected areas is a heterogeneous mosaic of smallholder rice farms, large tea estates, semi-urban large villages, small home gardens, and woodlots, with a high population density of 340/km² in Kaziranga (Shrivastava & Heinen, 2007). Elevation ranged between 40–110 m above sea level in the study area. The regional climate is strongly influenced by the North-eastern monsoon which breaks the dry season in April. During the peak of the monsoon in August monthly average rainfall is 301 mm (based upon the 1992–2002 average), and the overall mean annual rainfall

is 3,750 mm (Shrivastava & Heinen, 2007). The monsoon also sees maximum temperatures rise to 41°C and relative humidity reaches in excess of 90% (Vasu, 2002).

A2.4.2 *Ficus* trees survey

The data were collected between the 8th July and the 20th August 2009. Mature *Ficus* trees were systematically searched for within the study area by car and on foot. As the landscape was quite open, we conservatively estimate that $\geq 80\%$ were found. The location of each *Ficus* tree was marked with a Garmin GPS 60 device, accurate to within 15 m in open areas. The diameter at breast height (DBH) for each tree was measured (in centimetres) and the surrounding land-use was classified as tea estate, rice paddy, village woodlot, semi-urban, or forest edge. Rice paddy and semi-urban classes were considered to be proxies for high land-use intensity, tea estates and village woodlots were intermediate land-use intensity, and forest edge was low land-use intensity. Because only one fruiting fig was discovered in a rice paddy, this land-use type was excluded from statistical analysis. In all cases forest-edge trees were those that neighboured a protected area. The boundaries of the two protected areas were also marked using the same GPS device, and were used to measure the distance to the nearest protected area from each individual *Ficus* tree in kilometres.

A2.4.3 Frugivore surveys

Every afternoon, *Ficus* trees were checked for fruit ripeness, and when the crop was ripe, the frugivores visiting the tree were surveyed for 30 minutes the following morning. With this method, several trees could be surveyed in the same morning, which was necessary given the number of trees that were simultaneously ripe, and a tree would continue to be surveyed over several days until less than 50% of the crop remained. Frugivore surveys commenced at first light (usually around 04:20), and did not run beyond 07:40 (as bird activity typically decreased after that time). Surveys were conducted from a concealed position with a good

view c.15 m from the *Ficus* tree, and each individual bird that visited the tree was recorded. Bird species were classified as frugivores or non-frugivores based on observations during the surveys and the published literature (Shanahan et al., 2001; Grimmett et al., 2011).

A2.4.4 Statistical analysis

To compare bird visits to mammal- and bird-dispersed *Ficus* species, we compared the avian frugivore species richness and abundance of frugivores at mammal-dispersed (*F. racemosa*) and bird-dispersed (*F. religiosa*, *F. benghalensis*, *F. rumphii*, *F. benjamina*) *Ficus* trees. For trees with multiple surveys, we took the mean number of individuals of each species for comparisons of abundance. After exploring for normality, and using a Levene's test for equal variances, the differences between these groups were compared using an independent samples t-test (Field, 2009).

The effect of disturbance and distance on *Ficus* use by frugivorous birds was examined using an information-theoretic approach. The abundance of frugivores at scattered *Ficus* trees was analysed with a generalised loglinear model with Poisson errors (Burnham & Anderson, 2002) using the following input variables: distance from the nearest protected area, land-use type, tree DBH, tree species, and one second-order interaction term based on *a priori* hypotheses: land-use type*distance from the nearest protected area. None of the input variables in the models had more than 7 parameters. A second-order criterion, AIC_c, was used to select the best model due to the small ratio between the number of input variables and observations (Anderson et al., 2001).

To identify differences in community composition according to land-use type, we first computed a Morisita similarity index for the abundance of each frugivorous species in *Ficus* trees grouped by land-use category, with 200 bootstrap replications (Chao et al., 2008). This technique was preferred to multiple pairwise comparisons because it considers information

shared by more than two communities (Chao et al., 2008). For each of the common frugivore guilds recorded at the scattered *Ficus* trees (pigeons, barbets, starlings, and mynas), the mean abundance of each species was plotted against land-use type to discern assemblage configuration patterns. The statistical influence of distance and land-use intensity on the abundance of each of these species were tested using Multivariate Analysis of Variance (MANOVA) with scattered *Ficus* trees grouped into land-use type categories, which was used as a fixed factor, and tree distance from the nearest protected area as a covariate. Pillai's Trace was used to test for significance at the $p < 0.05$ level, and simple contrasts were conducted for land-use type (Field, 2009). All analyses were conducted using IBM SPSS Statistics 21 (IBM, 2012), except for the Morisita similarity index, which was calculated in SPADE (Chao & Shen, 2012).

A2.5 Results

A total of 326 *Ficus* trees were discovered in the landscape, of which 53 fruited and were surveyed during the study period. In total, 140 bird surveys were conducted, recording 76 species, 31 of which were frugivores. The most abundant species were the Yellow-footed Green Pigeon (2855 records), Chestnut-tailed Starling (2201 records), and Red-vented Bulbul (1165 records) (Supporting information, Section A2.10). The numbers of some flocking species recorded in a single survey were noteworthy, with highs of 430 Chestnut-tailed Starlings, 385 Spot-winged Starlings, and 298 Yellow-footed Green Pigeons arriving at individual *Ficus* trees within a 30-minute window (Table A2.1).

Table A2.1: The 10 largest flock sizes recorded during individual 30-minute surveys of scattered fruiting *Ficus* trees. A total of 140 surveys were conducted in the Kaziranga District of Assam, India.

Species	Number of birds
Chestnut-tailed Starling	430
Spot-winged Starling	385
Yellow-footed Green Pigeon	298
Yellow-footed Green Pigeon	200
Spot-winged Starling	167
Chestnut-tailed Starling	161
Chestnut-tailed Starling	150
Chestnut-tailed Starling	149
Chestnut-tailed Starling	140
Thick-billed Green Pigeon	124

Table A2.2: Differences in mean species richness and bird abundance at scattered fruiting *Ficus* trees according to fruit presentation. These data are derived from 140 surveys, 119 of which were at bird-dispersed trees, and 21 of which were at mammal-dispersed trees, in Kaziranga District of Assam, India. Bird-dispersed are those *Ficus* species with colourful, small, and odourless fruit; mammal-dispersed are those with dull, large, and odorous fruit. * indicates significant differences in an independent samples t-test, with a significance level of $p < 0.001$.

<i>Ficus</i> dispersal type	Richness (mean±SE)	Abundance (mean±SE)
Bird-dispersed	12.61±0.78*	70.92±12.57*
Mammal-dispersed	6.5±1.15	15.53±3.37

The comparison of frugivore assemblages visiting bird-dispersed and mammal-dispersed *Ficus* trees revealed that, on average, bird-dispersed *Ficus* trees received a higher number of frugivorous species than mammal-dispersed *Ficus* trees (Table A2.2). This difference was significant ($t_{(53)} = -3.82$, $p < 0.001$), with a medium effect size ($r = 0.4$). Frugivore abundance also varied according to *Ficus* dispersal mode. Although equal variances could not be

assumed ($F=6.03$, $p<0.05$), frugivorous birds were, on average, significantly more abundant at bird-dispersed *Ficus* trees than at mammal-dispersed trees ($t_{(47)}=-4.25$, $p<0.001$, $r=0.28$).

The information-theoretic evaluation strongly favoured a model with all the base variables plus the interaction term (Table A2.3), which had the lowest AIC_c value. The change in AIC_c scores and Akaike weights also suggested that there was essentially no support for any of the other models (Burnham & Anderson, 2002).

Table A2.3: Generalised loglinear model results with Akaike Information Criterion scores for variables affecting frugivore abundance at scattered fruiting *Ficus* trees. Data are derived from 140 avian frugivore surveys in Kaziranga District, Assam, India. Model input abbreviations are L=land-use type; S=*Ficus* tree species; D=distance from the nearest protected area; and DBH=*Ficus* tree diameter at breast height. L*D denotes a second-order interaction term between land-use type and distance from the nearest protected area. Other denotations: K=parameters in the model; MML=Maximum Log-likelihood; AIC_c =second-order Akaike Information Criterion score for finite samples; ΔAIC_c =the difference in AIC_c scores compared to the best performing model; and w_i =Akaike weight, the normalised model likelihoods (Burnham & Anderson, 2004). The best performing model is highlighted in bold font.

Model	K	MML	AIC_c	ΔAIC_c	w_i
L, S, D, DBH, L*D	5	-580.56	1199.98	0	1
L, S, D, DBH	4	-612.21	1253.99	54.01	0.000
L, D, L*D	3	-1194.96	2405.02	1205.04	0.000
L, D, S	3	-630.67	1286.84	86.85	0.000
L, S, DBH	3	-636.63	1298.77	98.78	0.000
S, D, DBH	3	-618.02	1257.81	57.82	0.000

The Morisita similarity index (Table A2.4) indicates the frugivorous communities found in *Ficus* trees of most land-use types were very similar (values closer to 1.0 indicates higher similarity; average pairwise comparison=0.77). In particular, the communities in tea estates were extremely similar to village woodlot (estimate±S.E.=0.94±0.084) and forest edge (0.92±0.086) *Ficus* trees, and fairly similar to semi-urban trees (0.85±0.12). The least similar

communities were those of semi-urban *Ficus* trees compared to village woodlot (0.6 ± 0.11) and forest-edge (0.52 ± 0.11) trees, which had only moderate similarity.

Table A2.4: Morisita similarity matrix of multiple communities (Chao et al., 2008), for frugivorous birds in *Ficus* trees, grouped by land-use type. Values are Morisita similarity estimate \pm standard error, with 200 bootstrap replications. Values closer to 1.0 indicate higher community similarity. Average pairwise comparison=0.77.

	Tea estate	Village woodlot	Semi-urban	Forest edge
Tea estate	1.0	0.94 \pm 0.084	0.85 \pm 0.12	0.92 \pm 0.086
Village woodlot		1.0	0.6 \pm 0.11	0.82 \pm 0.073
Semi-urban			1.0	0.52 \pm 0.11
Forest edge				1.0

The mean abundance charts revealed several patterns within each guild (Figure A2.1). Within the barbets, the Coppersmith Barbet was consistently the most abundant species in all land-use types, with Lineated and Blue-eared Barbets much more abundant in *Ficus* trees near protected areas. The pigeons showed a similar trend, with a much greater abundance and diversity of species at *Ficus* trees on the forest edge. No overall patterns were discernable for the starlings. Finally, for the mynas, the Hill Myna was recorded considerably more frequently in *Ficus* trees near the borders of protected areas, although the Common Myna was most common in the highly disturbed semi-urban landscape. This was reflected in the MANOVA results, which found no significant relationships between land-use type and distance from the nearest protected area for any of the species tested ($p > 0.05$), except for the Common Myna, which was significantly more common with increasing distance from the nearest protected area ($F_{(1)}=5.56, p < 0.05$).

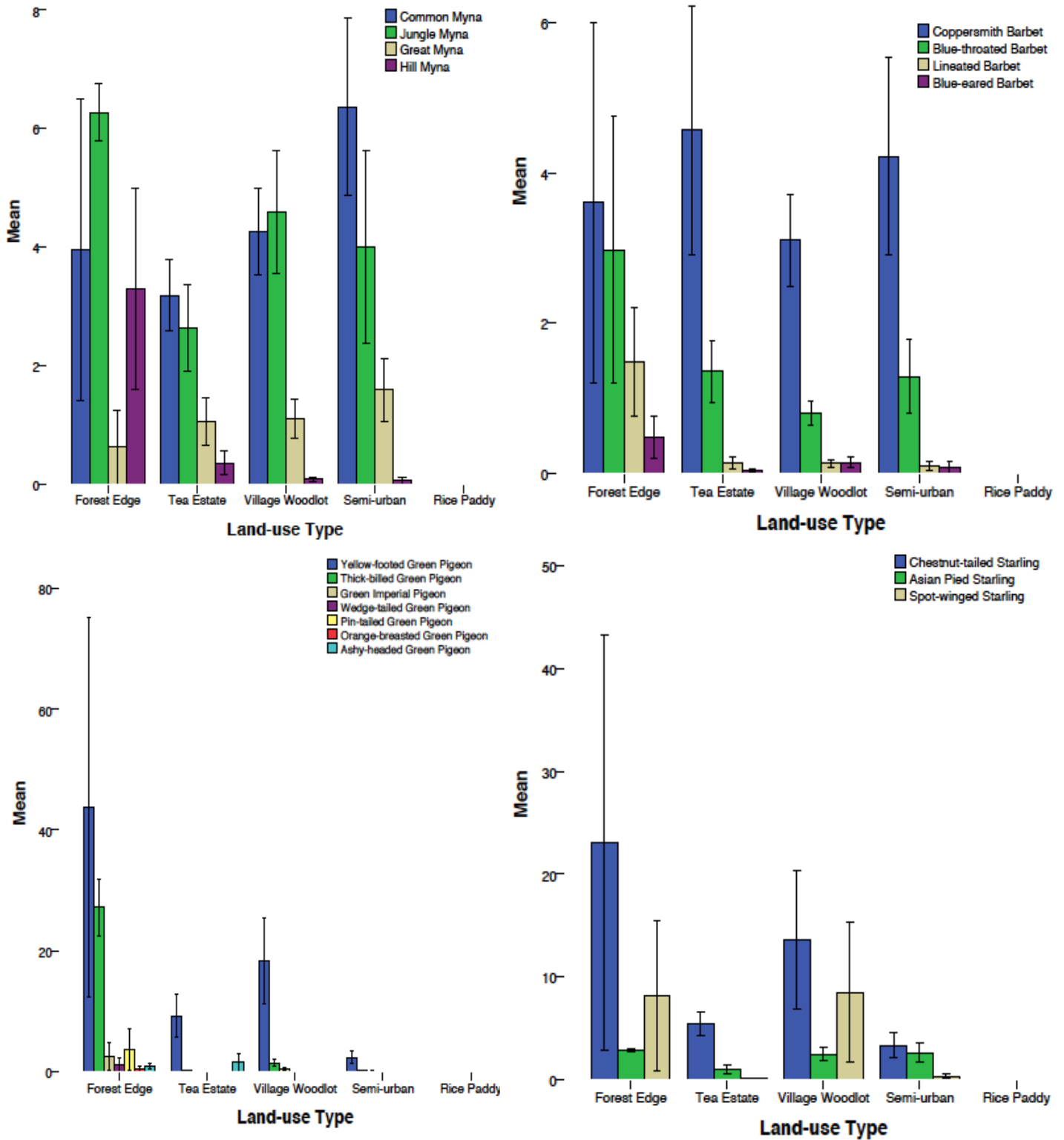


Figure A2.1: Mean abundances of frugivorous birds visiting *Ficus* trees in different land-use types. Bird species are split by guild, error bars are standard error. Data are derived from 140 avian frugivore surveys in Kaziranga District, Assam, India.

A2.6 Discussion

The results of this study suggest that biodiversity conservation beyond protected areas is a worthwhile pursuit. Moreover, it provides evidence that *Ficus* trees, scattered in human-modified landscapes, remain important as resources for frugivorous birds. Indeed, scattered *Ficus* trees appear to play a role in supporting migrant bird species, while also conserving frugivorous bird communities that survive independent from protected areas.

An interesting, yet unexpected, result of the bird surveys was the flocking behaviour observed at *Ficus* trees, with flocks of several hundred birds arriving in the space of half an hour and feeding on the *Ficus* fruit. While most of these species are locally resident all year round (Grimmett et al., 2011), some, such as the Spot-winged Starling, are long-distance migrants. Given the number of Spot-winged Starlings observed feeding at *Ficus* trees, it seems likely that *Ficus* fruit may constitute an important part of their diet on passage and on their nonbreeding grounds. Their presence at *Ficus* trees may also indicate their role in facilitating long-distance seed dispersal, and therefore regional *Ficus* distribution, as seeds consumed on the morning of a migratory stage may be deposited tens if not hundreds of kilometres from their parent tree. Although noted as strong fliers, no data currently exist on their gut passage times or daily movement distances by which to test this hypothesis (Feare & Craig, 1998; del Hoyo et al., 2009).

Our results found no support for the hypothesis that birds were feeding on mammal-dispersed *Ficus* fruit beyond protected areas due to a shortage in bird-dispersed *Ficus* fruit. Both the richness of avian frugivores and the abundance of frugivorous visitors were significantly higher in trees with small, bright, odorless fruit. This may be the result of a strong ecological link between fruit presentation and foraging preferences. Alternatively, the assumption that landscapes beyond protected areas have fruit shortages may be unfounded, and so avian frugivores have no need to revert to less desirable food sources (Luck & Daily, 2003).

Evidence for this view can be found in the abundance of *Ficus* trees in the landscape (occurring at a density of $3.17 \pm 0.26/\text{km}^2$ in the study area), of which the majority were bird-dispersed (as an indication, 78% of those trees that were surveyed were bird-dispersed).

The generalised loglinear model with information-theoretic criterion results indicated the model that best explained patterns in frugivore abundance was one which included all input variables. This suggests that no individual variable was overly important. In particular, it refutes the theory that distance and land-use intensity are important determinants in frugivore foraging patterns beyond protected areas, as the model with these variables plus their interaction term recorded the highest ΔAIC_c value (Burnham & Anderson, 2004).

The modeling results were supported by the guild-level MANOVA outcomes. There was no statistically significant relationships for land-use or distance to the nearest protected area (except for the Common Myna). The comparison of frugivorous community similarity estimates was also revealing. Although *Ficus* trees in more urban landscapes showed some considerable differences in avian frugivore community structure compared to those on the forest edge, other trees in tea estate or village woodlot settings had very similar communities to those trees bordering protected areas. Together with the model results, this suggests that the bird communities feeding on scattered *Ficus* trees are not only surviving beyond protected areas, but have no dependence on them. These results support the findings of other tropical countryside studies in India (Ranganathan et al., 2008), the Neotropics (Luck & Daily, 2003), and scattered *Ficus* trees in Kenyan farmland (Eshiamwata et al., 2006), indicating that tropical countryside landscapes may be important areas for biodiversity conservation (Perfecto & Vandermeer, 2008).

A2.7 Conclusion

Our results contain three important messages. Firstly, *Ficus* trees scattered beyond protected areas are important resources for avian frugivores, indicating their role in sustaining seed dispersal mechanisms in tropical countryside landscapes. Secondly, scattered *Ficus* trees may be important food resources for long-distance migrants, which may in turn deposit *Ficus* seeds over a broad geographical area. Finally, the strength of fidelity towards *Ficus* fruit with bird-dispersed characteristics, combined with the inability of the statistical tests to identify distance or disturbance as important effects, indicates that tropical countryside landscapes may provide higher quality habitat for frugivorous birds than commonly recognised.

A2.8 Acknowledgements

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A2.10 Supporting information

Table A2.5: List of frugivores recorded at scattered *Ficus* trees during the study, ordered by their mean abundance at the scattered *Ficus* trees. Values are the mean number of individuals of each species recorded per tree, followed by the standard error. Data are derived from 140 avian frugivore surveys in Kaziranga District, Assam, India.

Common name	Scientific name	Mean abundance±SE
Yellow-footed Green Pigeon	<i>Trenon phoenicoptera</i>	20.18±0.85
Chestnut-tailed Starling	<i>Sturnus malabaricus</i>	15.62±1.00
Red-vented Bulbul	<i>Pycnonotus cafer</i>	8.31±0.21
Spot-winged Starling	<i>Saroglossa spiloptera</i>	5.99±1.25
Common Myna	<i>Acridotheres tristis</i>	4.74±0.20
Jungle Myna	<i>Acridotheres fuscus</i>	4.72±0.29
Coppersmith Barbet	<i>Megalaima haemacephala</i>	4.06±0.20
Thick-billed Green Pigeon	<i>Trenon curvirostra</i>	3.15±0.61
Asian Pied Starling	<i>Sturnus contra</i>	2.49±0.24
Red-whiskered Bulbul	<i>Pycnonotus jocosus</i>	2.16±0.27
Great Myna	<i>Acridotheres cinereus</i>	1.31±0.15
Blue-throated Barbet	<i>Megalaima asiatica</i>	1.16±0.14
Rufous Treepie	<i>Dendrocitta vagabunda</i>	0.77±0.13
Ashy-headed Green Pigeon	<i>Trenon phayrei</i>	0.61±0.50
Asian Koel	<i>Eudynamys scolopacea</i>	0.61±0.12
Green Imperial Pigeon	<i>Ducula aenea</i>	0.49±0.17
Black-hooded Oriole	<i>Oriolus xanthornus</i>	0.46±0.12
Hill Myna	<i>Gracula religiosa</i>	0.31±0.18
Pin-tailed Green Pigeon	<i>Trenon apicauda</i>	0.26±0.49
Oriental Pied Hornbill	<i>Anthracoceros albirostris</i>	0.26±0.11
Lineated Barbet	<i>Megalaima lineata</i>	0.25±0.13
Large-billed Crow	<i>Corvus macrorhynchos</i>	0.21±0.16
Blue-eared Barbet	<i>Megalaima australis</i>	0.11±0.10
Wedge-tailed Green Pigeon	<i>Trenon sphenura</i>	0.10±0.23
Grey Treepie	<i>Dendrocitta formosae</i>	0.08±0.17
Golden-fronted Leafbird	<i>Chloropsis aurifrons</i>	0.05±0.11
Orange-breasted Green Pigeon	<i>Trenon bicincta</i>	0.04±0.16
Great Indian Hornbill	<i>Buceros bicornis</i>	0.03±0.12
Rose-ringed Parakeet	<i>Psittacula krameri</i>	0.03±0.13
Red-breasted Parakeet	<i>Psittacula alexandri</i>	0.01±0.09

APPENDIX 3:

Fig trees and conservation beyond protected areas

A3.1 Preface

Between my undergraduate dissertation and the start of the DPhil, my colleague Maan Barua conducted a study on isolated *Ficus* trees that merged ecological data with a questionnaire-based investigation. The questionnaire results helped shape some themes of analysis in the ethnographic (Chapter 10) and global social survey (Chapter 11) components of this study, while the frugivore surveys conducted by Jatin Tamuly were assimilated into Chapter 4. As the results of the study by Barua et al. provide the backdrop to sections of this thesis, the manuscript is included here as an appendix.

Authors: Maan Barua, H. Eden W. Cottee-Jones, Jatin Tamuly, Robert J. Whittaker

The co-author contributions were as follows. Conceived and designed the study: MB. Conducted the data collection: MB, JT. Analysed the data: MB. Wrote the paper: MB, HEWC-J, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This appendix is currently ready for submission, and will be submitted once there is confirmation from the lead author on which journal to submit to.

A3.2 Abstract

Conservation beyond protected areas is increasingly recognised as a valuable strategy. Critical to these efforts is an appreciation of the human–environment relationship, which moderates patterns of biodiversity in disturbed landscapes. However, few studies couple biogeographical and social analyses, which would help address conservation issues while generating new hypotheses. Here we survey the distribution of a critical component of tropical ecosystems, *Ficus* trees, in a modified landscape in Assam, India, and quantify their interactions with seed dispersing frugivores. We also administer a questionnaire in the local community to assess the values attributed to *Ficus* trees, their uses, and prospects for conservation. We found a decline in the richness of large-bodied frugivores at *Ficus* trees located further from protected areas, and received reports that these species were under higher hunting pressure than smaller-bodied species. The dominant values associated with *Ficus* trees were religious, which shaped their distribution in the landscape, and also influenced planting and conservation viewpoints. The joint study of social and biogeographical issues highlights the role *Ficus* trees play at the interface of biodiversity conservation and human belief systems, which may help identify prudent conservation strategies in landscapes beyond the protected area network.

Keywords Assam, conservation beyond protected areas, cultural values, *Ficus*, frugivory, India, disturbed landscape conservation, religious values, sacred trees

A3.3 Introduction

There is a growing recognition that conserving biodiversity beyond protected areas is a valuable strategy (Chazdon et al., 2009). Disturbed landscape conservation can reduce effective isolation (Ricketts, 2001), reduce the impact of edge effects (Jules & Shahani, 2003), and support assemblages that are independent of protected areas (Hughes et al., 2002). As more attention is being devoted to conservation in disturbed habitats, there is an urgent need to identify the best strategies. In order to inform decision-makers, we need to quantify patterns of biodiversity beyond protected areas, to build a greater understanding of the human–environment relationship, and to test ways of restoring landscapes quickly and inexpensively (Chazdon et al., 2009). The maintenance of networks of isolated trees in disturbed landscapes may offer an opportunity to develop these three themes (Fischer et al., 2010). Networks of scattered trees are a common feature in many landscapes around the world, and they are believed to be important ecological structures – providing habitat connectivity, softening edge effects, and increasing the species richness of agricultural landscapes (Manning et al., 2006).

While all isolated trees will contribute to this process, fruit trees are the best at attracting seed dispersers and so are likely to be the most valuable trees in ecosystem restoration. Of all the genera of fruit tree, figs of the genera *Ficus* (Moraceae) are considered to be among the most important (Terborgh, 1986). The 750 plus species of *Ficus* have a very wide geographical spread, and have been reported in the majority of tropical forest ecosystems around the world (Corner, 1962). Due to a co-evolved mutualistic relationship with their host-specific pollinator fig wasps, at least one fig in a population is in fruit at any given time. A combination of their unusual asynchronous fruiting cycle, large crop sizes, and global availability mean that over 1,200 tropical birds and mammals have been recorded consuming *Ficus* fruit (Shanahan et al., 2001). Many of these species are effective seed dispersers, and

so they play an important role in maintaining and restoring ecosystem function in tropical landscapes.

Figs are also important to the way humans relate to the environment, and may have greater cultural significance than that of other isolated trees (Mawdsley et al., 1998). In many regions, figs have a spiritual value due to their association with local deities and faiths. In India for example, *Ficus religiosa*, *F. benghalensis*, and *F. racemosa* are all believed to be manifestations of the God Vishnu (Chandrakanth & Romm, 1991) and larger figs are often converted into places of worship. As religious and cultural factors are believed to be important for conservation (Bhagwat & Palmer, 2009), the religious attributes of fig trees may secure their preservation during forest clearance.

Despite their importance, aspects of tropical biogeography and the human–environment relationship have rarely been studied in conjunction. Therefore, we sought to develop an understanding of the biogeographical and social value of *Ficus* trees in disturbed landscapes by studying a network of isolated fig trees in Assam, India, and assessing their value as a tool for conservation beyond reserves. To this end, we devised two areas for research: 1) How are frugivory patterns influenced by landscape factors? What roles do isolated fig trees play in sustaining frugivory? 2) What are the economic and socio-cultural values associated with fig trees? And do they contribute to the survival of remnant fig trees in the agricultural landscape? How might these values be harnessed to inform modes of conservation outside protected areas in tropical country contexts?

A3.4 Methods

A3.4.1 Study area

This study was conducted in the agricultural matrix surrounding Kaziranga National Park (26°35'–26°45'N and 93°05'–93°40'E) and the remnant forest patch at the Panbari Reserve Forest in Assam, India. The non-reserve matrix consists of a heterogeneous mixture of large, commercial tea estates, small village home gardens interspersed with very small woodlots (<0.25 ha) that retain some amount of native vegetation, rice paddy cultivation, and agricultural pastures. Land-use is diverse and divided among many small landholdings. Most of the conversion of forests to tea plantations occurred over 100 years BP.

A3.4.2 *Ficus* census

Mature *Ficus* trees within the landscape were systematically searched for on foot along all major roads, in paddy fields, village woodlots, home gardens and tea plantations. We did not count *Ficus* trees at the epiphytic stage as they were extremely abundant and it was difficult to get exact measures of their number. The height, DBH, and crown diameter of *Ficus* trees were measured, and their locations marked with a GPS unit. For each tree, the following were also recorded: surrounding land-use intensity (within a 100 m radius circle centred on the fig tree), habitat type (simplified into three distinct matrix types: village home garden, tea plantation, and rice paddy), the distance to the nearest forest patch (grouped into near or far sites according to the median distance of samples, 2,482 m), and the presence/absence of temples, shrines, or other religious structures. These efforts did not locate every *Ficus* in the research area; the smallest DBHs were certainly under-represented. Nonetheless, a conservatively estimated $\geq 80\%$ were recorded.

A3.4.3 Frugivore sampling

Frugivorous bird activity at 59 fruiting *Ficus* trees was sampled with three-hour point counts commencing at daybreak (generally 04:00–05:30 depending on the time of year). Fruit abundance at each fruiting tree was estimated immediately prior to collecting bird data by looking at the left, centre, and right of the mid-canopy with one frame of 8×42 binoculars and estimating the abundance of fruit in each, before averaging the three. During the three-hour observation period, the number of birds of each species was recorded. Species that could not be identified were not included in the estimation of species richness, so all reported values are conservative.

A3.4.4 Questionnaire design

We initially conducted in depth semi-structured interviews with residents within the local community to explore local perceptions of figs (Browne-Nuñez & Jonker, 2008). This involved asking people what they thought about *Ficus* trees, the number of species they recognised, and the uses and values associated with them. These interviews were later analysed to identify key themes and patterns (Ryan & Bernard, 2003), and a structured questionnaire was designed thereafter. The questions were translated into Assamese and then back translated by an independent translator in order to test the linguistic appropriateness of the survey instrument.

The questionnaire was administered between April 2010 and October 2010. The study was restricted to the Assamese, Hindu-speaking community as they were the most prominent social group in the area. A household was randomly selected in a village and subsequently every third house on the right from there onward was sampled. Only individuals above the age of 18 were interviewed. The objectives of the study were explained beforehand and individuals were asked to either fill in the questionnaires or, as was more often the case (90%

of the respondents), respond to the questions verbally. Clarifications were made if individuals were unsure what a question meant. All interviews were conducted in Assamese, and as the interviewers were native speakers of the language, interpreters were not used.

A3.4.5 Statistical analysis

The trees discovered by the *Ficus* census were grouped into five quintiles according to DBH, and small trees were considered to be younger than larger ones (Duvall, 2007). The abundance of *Ficus* trees within land-use categories and by species was then compared using a chi-squared analysis based on the size of each quintile, and how the expected and observed numbers of *Ficus* per quintile differed.

To investigate the determinants of frugivorous bird abundance in the *Ficus* trees, we ran a general linear model with the log transformed number of individual frugivores as the response variable, and log transformed *Ficus* fruit crop size and the distance of the *Ficus* tree from the nearest forest as explanatory variables. We then divided our frugivorous species into four sub-groups: forest-dependent species, forest-generalist species, forest-specialist species, and large-bodied species. Forest-dependence was assessed through consultation with the literature (Grimmett et al., 2011) and our own field experience. Species were classified as small- or large-bodied using a median body mass of 37.6 g, following Blackburn and Gaston's (1994) analysis of 6,209 bird species.

The social survey data were analysed using nonparametric methods as none of the variables were normally distributed. Respondents were asked to list economically important trees, and the relative economic value of these trees was estimated by ranking each species mentioned using a simple score (number of times mentioned ÷ total number of respondents). The final scores were tested for significant differences using a Cochran's Q test. Cochran's Q test was also used to test the significance of differences between economic, social, and religious

values respondents' associated with *Ficus* trees, their views on where *Ficus* trees should grow, how they should be conserved, and which trees have the greatest religious attributes. Chi-squared tests were used to examine opinions concerning who should be responsible for *Ficus* conservation, human-uses attributed to *Ficus*, and why they survived in the landscape.

A3.5 Results

A3.5.1 *Ficus*–frugivore results

A total of 473 *Ficus* trees were mapped in the landscape, of which the DBH of 437 were calculated. The DBH of some trees were omitted due to poor accessibility and difficulty in measuring the base due to dense vegetation. This sample of 437 (n=437) was considered in the final analysis. The mean DBH of these 437 *Ficus* trees was 3.61 (SE=0.10). The number of trees per quintile ranged from 84 to 92 (Table A3.1). There were no differences in the distribution of different *Ficus* ages in home gardens or in tea estates, where representation of all DBH classes was equal (Table A3.2). However, in paddy fields older trees (Quintile 5) were under-abundant, and trees in younger classes were over-abundant.

Table A3.1: *Ficus* DBH quintile characteristics. All *Ficus* DBH records (n=437) were split into five groups of approximately equal class size to compare size distributions.

Quintile	<i>Ficus</i> DBH	<i>Ficus</i> per Quintile
1	≤0.32–0.62	87
2	0.62–0.96	92
3	0.96–1.21	89
4	1.21–1.62	85
5	≥1.62	84

Of the 437 individual *Ficus* trees mapped in the study landscape, 64 trees had shrines or temples associated with them. There was a significant difference in the proportion of shrines in each DBH quintile category: trees with higher DBH (Quintiles 4 and 5) had a greater proportion of shrines, whereas those with smaller DBH had fewer shrines (Table A3.3).

Similarly, there were a greater proportion of shrines or temples on *F. benghalensis*, *F. religiosa* and *F. rumphii* than other *Ficus* species. *F. benghalensis* and *F. rumphii* trees that were used as shrines also had a larger DBH than those that were not. The mean DBH of *F. religiosa* trees with shrines was slightly larger than those without, but the difference was not significant.

Table A3.2: *Ficus*–habitat associations per quintile (n=437). The distribution of *Ficus* trees from different DHB quintiles was analysed with reference to land-use category and *Ficus* species to detect cases where certain size classes were under- or over-represented. Symbols used to indicate statistical significance: +++=over-abundant, $p<0.001$; ***=under-abundant, $p<0.001$. ¹ $\chi^2=5.45$, df=4, $p=0.24$; ² $\chi^2=7.24$, df=4, $p=0.12$; ³ $\chi^2=20.88$, df=4, $p<0.001$; ⁴ $\chi^2=3.55$, df=4, $p=0.47$; ⁵ $\chi^2=20.32$, df=4, $p<0.001$; ⁶ $\chi^2=4.88$, df=4, $p=0.18$; ⁷ $\chi^2=28.05$, df=4, $p<0.001$; ⁸ $\chi^2=6.84$, df=4, $p=0.15$.

		All individuals	Q1	Q2	Q3	Q4	Q5
Land-use category	Home gardens ¹	164	35	32	43	28	26
	Tea estates ²	157	20	34	28	39	36
	Paddy fields ³	80	30 ⁺⁺⁺	20	11	12	7 ^{***}
<i>Ficus</i> species	<i>Ficus benghalensis</i> ⁴	66	11	18	14	14	9
	<i>Ficus religiosa</i> ⁵	136	21	39	39	25	12 ^{***}
	<i>Ficus racemosa</i> ⁶	17	0	3	4	8	2
	<i>Ficus microcarpa</i> ⁷	38	7	4	1	6	20 ⁺⁺⁺
	<i>Ficus rumphii</i> ⁸	172	46	28	28	32	38

The frugivore surveys revealed that the distance a fig tree was from the forest affected the composition of frugivores visiting it. In particular, species that are characterised as forest-specialists were significantly less numerous as the distance from the nearest forest increased ($\beta=-0.562$, $p<0.001$). Large-bodied frugivores were also more vulnerable to distance effects ($\beta=-0.049$, $p=0.032$), suggesting that fewer large bodied forest-specialists forage in distant fig trees than in figs located close to the forest (Table A3.4).

Table A3.3: Distribution of shrines according to *Ficus* DBH and species. The presence of shrines of *Ficus* trees of different DBH size and species was analysed by identifying DBH quintiles (Q) or species where there were significantly more or less shrines than expected. Symbols used to indicate statistical significance: +++=over-abundant, $p < 0.001$; ***=under-abundant, $p < 0.001$; ++=over-abundant, $p < 0.01$; **=under-abundant, $p < 0.01$.¹ $\chi^2 = 11.49$, $df = 4$, $p < 0.05$; ² $\chi^2 = 44.75$, $df = 5$, $p < 0.001$.

	Q1	Q2	Q3	Q4	Q5		
Religious shrine present ¹	5**	13	11	17 ⁺⁺	18 ⁺⁺		
<i>Ficus sp.</i>	<i>benghalensis</i>	<i>elastica</i>	<i>religiosa</i>	<i>benjamina</i>	<i>racemosa</i>	<i>microcarpa</i>	<i>rumphii</i>
Religious shrine present ²	18 ⁺⁺⁺	1***	23 ⁺⁺⁺	1***	-	4***	17 ⁺⁺⁺

Table A3.4: General linear model of frugivorous bird abundance in *Ficus* trees in Assam, divided into five categories, with *Ficus* fruit crop size and the distance of the *Ficus* tree from the nearest forest as explanatory variables. Body weights of species were \log_{10} transformed; a median of 1.58 (corresponding to 37.6 g) taken to classify species as small- or large-bodied (based on masses of 6,209 species; Dunning, 1993; Blackburn & Gaston, 1994).

Response variable		β	t	p
All species	$R^2=0.003$			$p<0.05$
	Log ₁₀ number of individuals	-0.04	-1.96	0.05
		0.03	1.22	0.22
Forest-dependent species	$R^2=0.01$			$p<0.05$
	Log ₁₀ number of individuals	-0.10	-2.80	0.01
		0.01	0.26	0.80
Forest-generalist species	$R^2=0.003$			$p=0.052$
	Log ₁₀ number of individuals	-0.04	-1.57	0.12
		0.03	1.41	0.16
Forest-specialist species	$R^2=0.32$			$p<0.001$
	Log ₁₀ number of individuals	-0.56	-4.30	0.00
		0.01	0.04	0.97
Large-bodied species	$R^2=0.004$			$p<0.05$
	Log ₁₀ number of individuals	-0.05	-2.42	0.03
		0.03	1.09	0.28

A3.5.2 Social survey results

A total of 278 questionnaires (n=278) were completed, with an overall response rate of 90%. The majority of the respondents were male (89.5%; n=247) as our sampling was generally through households and men are considered to be the spokespersons in the community. The mean age of the respondents was 37 years (range from 18 to 95). Average monthly income ranged from INR0 to INR15,000 (mean monthly income=INR4,700, equivalent to

US\$76.13). The average education of the respondents was nine years (ranging from no education to 17 years).

When discussing the economic importance of trees, a total of 58 species were mentioned by respondents (Table A3.5). Using the simple score index, mango ranked highest (0.71), followed by jackfruit (0.53), teak (0.42), coconut (0.32) and betel nut (0.31). *Ficus* scored poorly: *F. religiosa* had a score of 0.04, followed by *F. benghalensis* (0.02), *F. rumphii* (0.01) and *F. racemosa* (0.01).

Table A3.5: Trees mentioned by respondents, ordered by relative economic importance. Rank scores were calculated by dividing the number of times a tree was mentioned by the total number of respondents.

	Species	Family	Local Name	Rank
1.	<i>Mangifera indica</i>	Anacardiaceae	Aam	0.712
2.	<i>Artocarpus heterophyllus</i>	Moraceae	Kathal	0.529
3.	<i>Tectona grandis</i>	Verbenaceae	Segun	0.424
4.	<i>Cocos nucifera</i>	Aracaceae	Narikol	0.317
5.	<i>Areca catechu</i>	Aracaceae	Tamul	0.306
6.	<i>Gmelina arborea</i>	Verbenaceae	Gamari	0.284
7.	<i>Psidium guajava</i>	Myrtaceae	Madhuri	0.183
8.	<i>Cedrela toona</i>	Meliaceae	Poma	0.137
9.	<i>Syzigium</i> spp.	Myrtaceae	Jamu	0.129
10.	<i>Musa</i> spp.	Musaceae	Kol	0.115
28.	<i>Ficus religiosa</i>	Moraceae	Ahot	0.043
41.	<i>Ficus benghalensis</i>	Moraceae	Bor	0.022
44.	<i>Ficus racemosa</i>	Moraceae	Dimoru	0.018
45.	<i>Ficus rumphii</i>	Moraceae	Jori	0.018

Responses to the question “do *Ficus* trees have any value?” showed that 70% (n=191) felt that these trees had some value, whilst 30% (n=82) said they didn’t. A range of values and uses were associated with these trees, including religious value, use as firewood and timber, fodder for cattle, as food for birds or animals, and social/community benefits (Figure A3.1). The most frequent value associated with *Ficus* was religious, accounting for 46% of the responses (n=129). Religious values included use of some part of the fig in religious

ceremonies or referred to innate religious attributes, such as their association with ancestral spirits). This was followed by social values or community benefits such as markers of important places, resting spaces, etc. (6.47%; n=18), and as fodder for cattle (5.76%; n=16). Differences between the values mentioned were significant (Cochran's $Q=5.65$, $df=7$, $p<0.001$).

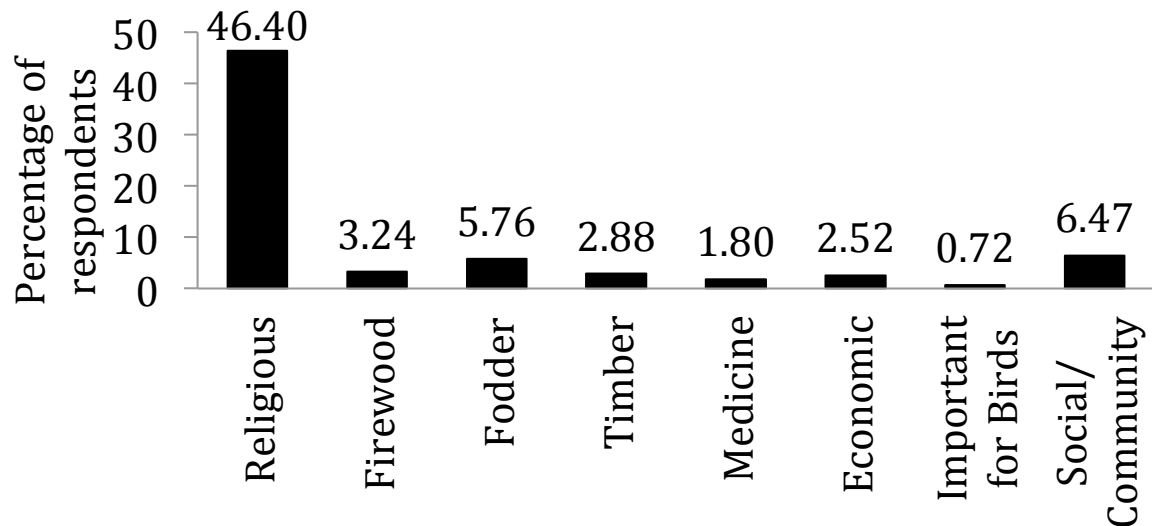


Figure A3.1: Values and uses associated with *Ficus*, as reported in the questionnaires (n=278). Results obtained from a survey of 278 local inhabitants of the area surrounding Kaziranga National Park, Assam, India. Questionnaires were administered in person, face-to-face, were conducted in Assamese, and asked 17 questions concerning the status of, and attitudes towards, *Ficus* in the study area. Differences in group sizes were significant ($\chi^2_{(7)}=529.94$, $p<0.001$).

Fifty-three percent (n=147) of the respondents said they cut *Ficus* trees, whilst 47% (n=131) said they didn't (Figure A3.2). Most people said they either cut branches or plucked leaves from the tree. Less than 1% said they cut the whole tree down or removed saplings. The main reason for plucking leaves was for use in religious ceremonies, whilst branches were cut either to obtain firewood or when there was excessive growth and it interfered with peoples' activities.

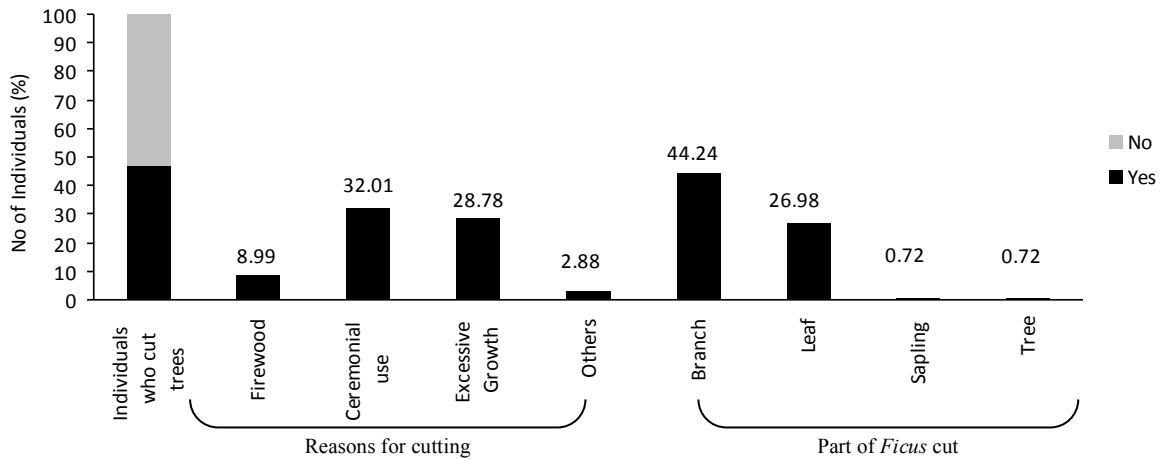


Figure A3.2: Responses to questionnaire questions about cutting *Ficus* trees: “do people cut *Ficus* trees? Why? What part of the tree do they cut?” These questions were asked as part of a survey concerning the status of, and attitudes towards, *Ficus* around Kaziranga National Park in Assam, India. The questionnaire consisted of 17 semi-structured questions, and was conducted in Assamese with 278 respondents.

It was difficult to estimate the number of individuals of each frugivore killed when visiting *Ficus* trees, as people were not willing to disclose such information. This is reflected by the number of respondents who were unwilling to respond (5.40%; n= 15), gave conservative answers such as “no birds are killed” (17.99%; n=50), or gave vague replies of “all birds are killed” (28.78%; n=80). However, it was possible to identify the most vulnerable species through triangulation, i.e. asking people which species others killed in their vicinity. Green pigeons (*Treron* spp.) appeared to be the most common target with 30.58% (n=85) mentioning the group. Other frequently cited birds were also Columbines – Green Imperial Pigeon (*Ducula aenea*) (8.98%; n=25) and doves (*Streptopelia* spp.) (11.51%; n=32), while hornbills also featured on the list (9.71%; n=27). Most birds mentioned were large-bodied, suggesting that large-bodied species may be more vulnerable when venturing beyond the forest edge to feed on *Ficus*.

A number of reasons for killing birds were mentioned. These included killing for meat (70.86%; n=197), killing for fun (6.47%; n=18), and killing because they are pests (0.72%;

n=2). Some respondents said these birds were killed “because of their large size” (1.80%; n=5), a feature related to killing birds for meat. Some individuals gave guarded replies, saying “no birds are killed” (1.08%; n=3) or refused to comment (5.76%; n=16).

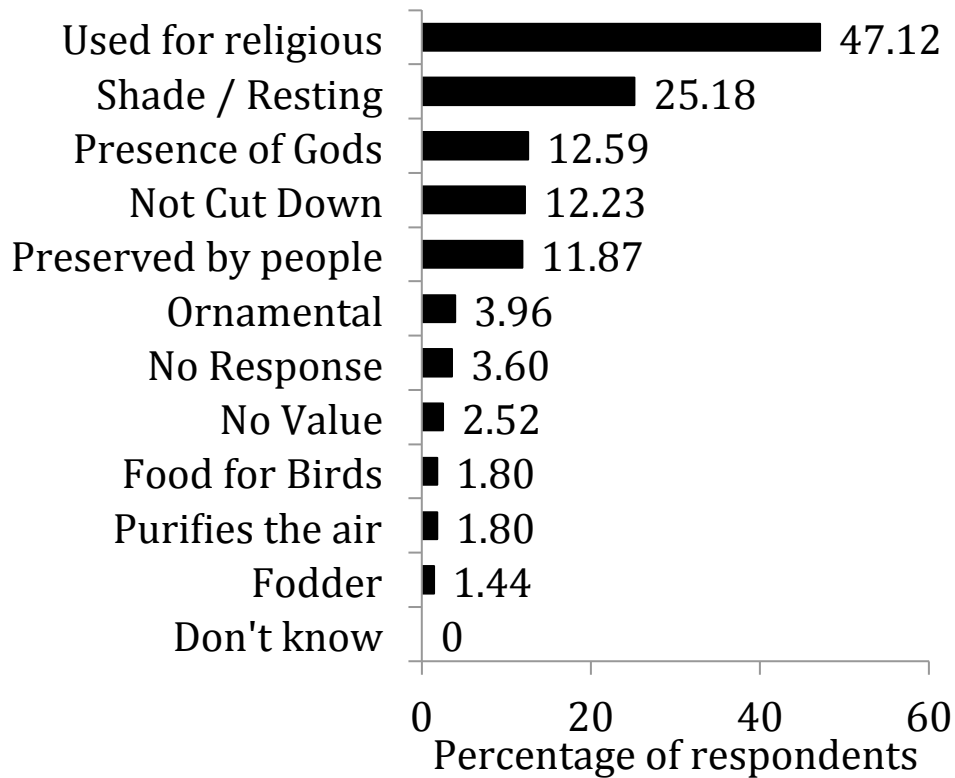


Figure A3.3: Questionnaire responses to “why do *Ficus* trees remain in the landscape?” The survey consisted of semi-structured interviews with 278 residents around Kaziranga National Park, Assam, India. Interviews were conducted in Assamese, and asked 17 questions concerning the status of, and attitudes towards, *Ficus* in the study area. Differences in group sizes were significant ($\chi^2_{(10)}=474.80, p<0.001$).

A range of explanations were given when people were asked why *Ficus* trees remained in the landscape (Figure A3.3). Their use in religious ceremonies was the most frequent response (47.12%; n=130), followed by their social value as places of shade or for resting (25.18%; n=70). Respondents also said that figs remained in the landscape because they were inhabited by gods or spirits (12.59%; n=35). Other explanations were more simplistic and direct, including: “because they are preserved by people” (11.87%; n= 34) and “because no one cuts them down” (12.23%; n=34).

More people attributed religious values to *F. religiosa* (91%; n=253), followed by *F. benghalensis* (87%; n=241), and *F. rumphii* (83%; n=231). Differences in religious values for different species were significant (Cochran's $Q=1.03$, $df=3$, $p<0.001$). *F. racemosa* scored lowly for community values (18%; n=51), and had the lowest religious attributes (67%; n=185) when compared to other *Ficus* species. Social values ascribed to different *Ficus* species were also significant (Cochran's $Q=1.07$, $df=3$, $p<0.001$). However, there were no differences amongst *Ficus* species in terms of their use as cattle fodder (Cochran's $Q=0.00$, $df=3$, $p=1.00$).

Most respondents said all *Ficus* trees had religious attributes, regardless of their growing location (71.58%; n=199). Others mentioned specific localities: *Ficus* associated with temples (24.10%; n=67), those in villages (5.40%; n=15), and trees by the roadside (5.04%; n=14). Differences in referral to these localities were significant (Cochran's $Q=78.77$, $df=2$, $p<0.001$), with temple trees scoring higher than village trees or trees by the roadside.

Most people felt that *Ficus* in village spaces or near the national highway (where a lot of *Ficus* were distributed) were public property (83% and 71% respectively). Respondents also said that the onus of conserving these trees was on the public. However, there were differences in opinion as to whether trees in villages and those by the highway were public property (villages $\chi^2_{(1)}=121.78$, $p<0.001$, national highway $\chi^2_{(1)}=50.82$, $p<0.001$). Similarly, more people thought that trees by the highway were the government's property as opposed to those in village spaces (villages $\chi^2_{(1)}=160.95$ $p<0.001$, national highway $\chi^2_{(1)}=53.24$, $p<0.001$). More respondents said it was their duty to conserve *Ficus* trees in villages (22.06%), as opposed to those by the highway (no respondents; 0%).

When asked "what measures should be taken to conserve *Ficus* trees?", the majority of the respondents (58%) said they didn't know or didn't respond to the question. Measures that were cited included planting saplings, preventing *Ficus* trees from being cut down, taking

care of saplings, and protecting *Ficus* from domestic animals (such as cattle and goats). A few respondents (3.60%) said that people should be made more aware of *Ficus* and its conservation values.

Only 47% of the respondents were willing to plant *Ficus* trees. There was a local belief that one should not plant *Ficus* trees unless for some religious purpose, and this may have been a contributing factor to the low rate of responses in willingness to plant *Ficus*. Moreover, the fact that very few people had them in their gardens, and when present these grew by chance, suggest that planting might not work unless initiated by third-party actors. More people (30.58%; n=85) thought *Ficus* should be planted by the roadside, as opposed to other village spaces (26.62%; n=74) or in their own homes (8.63%; n=24) (Cochran's $Q=52.86$, $df=2$, $p<0.001$). Whilst a few people (7.55%; n=21) said that the prevention of *Ficus* cutting was one way of conserving them, fewer people were willing to prevent cutting of *Ficus* that belonged to other individuals (58.63%; n=163) as opposed to those standing by the roadside (79.1%; n=220) and those in temples (81.29%; n=226) (Cochran's $Q=1.09$, $df=2$, $p<0.001$).

A3.6 Discussion

Our frugivore survey results indicate that the distance of a *Ficus* tree from the forest has a significant effect for all bird groups except forest-generalist species (Table A3.4). Forest-dependent and forest-specialist species were significantly rarer as distance from the forest increased, which limits the role isolated *Ficus* trees can play in their conservation at the landscape level. Similar results have been reported for *F. thonningii* trees in Kenya, with fewer frugivore species visiting trees in highly disturbed sites (Kirika et al., 2008). Of more concern, however, is the decline in large-bodied frugivore species at distant *Ficus* trees. These species are especially important in facilitating seed dispersal over long distances, and many large-seeded species are dependent on them (Sekercioglu, 2006; Jordano et al., 2007). The social survey results indicate that hunting pressure may be a major factor in their lower

occurrence at distant figs, which would be consistent with the findings of several other studies (da Silva & Tabarelli, 2000; Owens & Bennett, 2000; Peres, 2000). Peres (2000), for example, found that persistent hunting markedly reduced the densities of large-bodied game species, while da Silva and Tabarelli (2000) found that large, wide-gaped fruit-eating birds were more vulnerable to human disturbance than narrow-gaped birds in a highly fragmented landscape. As in these cases, a decline in large-frugivores visiting isolated *Ficus* trees is likely to be linked to a deterioration in seed dispersal and associated ecological functions in matrix landscapes.

Frugivory patterns are also, of course, shaped by the configuration of mature *Ficus* trees. We found several trends in fig distributions in the matrix landscape, with figs more likely to occur along the sides of highways or in communal village areas, and larger figs less likely to survive in areas with high intensity land-use, such as rice paddies. Even in cases where figs do survive, they are likely to have branches removed should they interfere with crop production, or for use as firewood. However the major reason for cutting part of a *Ficus* tree was to obtain leaves or branches for religious purposes, and it is the intersection of *Ficus* and belief that may provide a good example of cultural values contributing to the survival of an organism in a human-modified landscape. This reflects the notion that biological diversity is connected to an integrated social-ecological system (Berkes & Folke, 1998), which in many other areas around the world, helps to create heterogeneous cultural landscapes, aligning production with conservation (Robson & Berkes, 2010).

Over 70% of respondents attributed a religious value to *Ficus* trees, and while it was unevenly distributed among species, this association may help explain the abundance of *Ficus* trees in the agricultural landscape when it provides little economic benefit. The use of fig trees for religious ceremonies, and the belief that figs are inhabited by gods or spirits, were frequently cited as reasons for the survival of *Ficus* in the landscape. The conservation

of *Ficus* trees, and therefore frugivorous birds, for these religious reasons confers many of the attributes of sacred groves to *Ficus* trees (Bhagwat & Rutte, 2006). Sacred groves, areas of habitat that are locally conserved for their religious significance, are increasingly recognised as important sites for biodiversity conservation in India (Bhagwat et al., 2005) and elsewhere (Dudley et al., 2009). Our results suggest that networks of isolated *Ficus* trees may be conserved, and help conserve biodiversity, in a similar manner, albeit at a smaller scale. Here the interface between cultural elements of the human–environment relationship, the resulting *Ficus* distribution configuration, and the *Ficus*–frugivore relationship, offer an opportunity to conserve key ecological functions in a network of individual tree-scale sacred sites. Situating *Ficus* trees within this framework may be a promising avenue to help understand their role in conservation in agricultural landscapes.

However, the same cultural factors that help conserve *Ficus* trees are also responsible for shaping, and in some cases limiting, their abundance and distribution. The religious significance of fig trees restricted *Ficus* planting to religious ceremonies in the study area, which may preclude the use of *Ficus* in large-scale tree planting conservation initiatives. Their sacredness may have wider implications for biodiversity offsetting (Maron et al., 2012), as the religious values associated with large, old *Ficus* trees may be hard to compensate by planting another tree of the same species elsewhere. The link between *Ficus* trees and religion may also reduce the effectiveness of individual trees in supporting frugivores. Many people believed that trees with temples or trees by the roadside were of particular religious importance, and so are more likely to be conserved, even though the levels of human disturbance at such trees is likely to deter birds from visiting (Benítez-López et al., 2010). And while the religious importance of *Ficus* trees was frequently cited, so too was the need to manage their growth when they came into conflict with economic imperatives. Cutting excessive growth was reported in peoples' home gardens or in paddy fields, where shade

acted as a constraint to agricultural productivity. The conflict between agricultural incentives and religious imperatives is reflected by the paucity of older trees in paddy field habitats, suggesting that their sacred status may not be sufficient to ensure the conservation of *Ficus* trees in production settings.

A3.7 Conclusion

Despite this, our results demonstrate the importance of culturally attuned approaches to conservation in human landscapes. Patterns of biodiversity in our study area were closely related to human attitudes and belief systems, affecting the present configuration of important fruit resources in an agricultural landscape, while also strongly influencing future dynamics in landscape-scale *Ficus* distributions, species abundances, and age profiles. Harnessing this appreciation of cultural values through the conservation of sacred trees may help strengthen ties between man and nature, while also forging landscape-scale conservation initiatives that are sensitive to, and driven by, cultural factors. Similar studies of culturally and economically important species in human landscapes around the globe may offer additional promising conservation opportunities.

A3.8 Acknowledgements

First of all, we would like to thank all the participants who took time to answer our questionnaires. We owe our gratitude to Nakib Ali, Taz Ahmed, Tarun Gogoi, Polash Bora, Diganta Gogoi, Gokul Munda, Biju Hazarika, and Buddheswar Konwar for their assistance with the field work. We are also grateful for the support received from Manju Barua, Kamini Brua, and Dilip Gogoi in Assam. We would like to thank Paul Jepson, Bibhab Kumar Talukdar, Bhupendranath Talukdar, Sushrut Jadhav, and Daniel Gurdak for their comments and suggestions at various stages of the project. Finally, we are very grateful to The Rufford Small Grants Foundation for funding this study.

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APPENDIX 4:

Authorship statements for co-authored papers

In accordance with the regulations set out in the GSO.21 examination notes, letters from each co-author, detailing their role in the relevant manuscripts, and consenting to the inclusion of the relevant manuscripts in this thesis, are enclosed in this appendix. The letters are presented in the same order that the authors appear in through the thesis.

SCHOOL OF GEOGRAPHY AND THE ENVIRONMENT

Tom J Matthews

DPhil candidate

Oxford University Centre for the Environment,

South Parks Road, Oxford OX1 3QY, UK

+44(0)1865 285070

thomas.matthews@ouce.ox.ac.uk www.geog.ox.ac.uk/research/biodiversity



Isolated *Ficus* trees and conservation in human-modified landscapes

Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscripts presented as Chapters 4, 5, 6, 9, and 11 within this thesis, for which I am a co-author, are substantially the work of the first author, Eden Cottee-Jones. My role has been limited to statistical assistance and commenting on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

A handwritten signature in black ink, appearing to read 'Tom J Matthews'.

22nd September 2014



UNIVERSITY OF OXFORD
DEPARTMENT OF ZOOLOGY
Tinbergen Building, South Parks Road, Oxford OX1 3PS

Direct line: (01865) 271 173
e-mail: tom.bregman@zoo.ox.ac.uk

From:
Tom P Bregman
DPhil student
Edward Grey Institute

Isolated *Ficus* trees and conservation in human-modified landscapes

Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscripts presented as Chapters 4 and 5 within this thesis, for which I am a co-author, are substantially the work of the first author, Eden Cottee-Jones. My role has been limited to assisting with data collection at the Natural History Museum, Tring, and commenting on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

Tom Bregman

A handwritten signature in black ink that reads 'tbregman'.

22nd September 2014

SCHOOL OF GEOGRAPHY AND THE ENVIRONMENT
INTERNATIONAL GRADUATE SCHOOL

Maan Barua
Research and Teaching Fellow

OUCE, South Parks Road
Oxford OX1 3QY
UK
maan.barua@ouce.ox.ac.uk

22 September, 2014

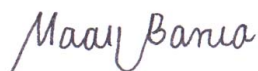
Isolated *Ficus* trees and conservation in human-modified landscapes

Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscript presented as Chapter 4 within this thesis, for which I am a co-author, is substantially the work of the first author, Eden Cottee-Jones. My role has been limited to providing a portion of the survey data from Assam and commenting on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

Jatin Tamuly, who also appears as a co-author in Chapter 4, conducted the majority of the surveys that I contributed towards the manuscript. Although circumstances mean that he is unable to confirm his co-authorship status in writing, I have discussed the matter with him in person, I would like to pass on his consent concerning the inclusion of Chapter 4 in this thesis.

I also consent to the inclusion of Appendix 3, for which I am the first author, in this thesis. Eden has made a considerable contribution to the direction of this research and to writing the manuscript. His efforts to prepare it for submission will ensure it begins the peer-review process soon.



Maan Barua

School of Geography and the Environment
University of Oxford

SCHOOL OF GEOGRAPHY AND THE ENVIRONMENT

Robert J Whittaker
Professor of Biogeography
Oxford University Centre for the Environment,
South Parks Road, Oxford OX1 3QY, UK
Direct tel: +44(0)1865 275845 Reception: +44(0)1865 285070
robert.whittaker@ouce.ox.ac.uk www.geog.ox.ac.uk/research/biodiversity



Isolated *Ficus* trees and conservation in human-modified landscapes

Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscripts presented as Chapters 4–11 within this thesis, along with Appendices 1–2, for which I am a co-author, are substantially the work of the first author, Eden Cottee-Jones. My role has been limited to supervisory input and comments on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

Robert J Whittaker

22nd September 2014



**G.B. Pant Institute of Himalayan
Environment & Development**

Kosi-Katarmal, Almora – 263643, Uttarakhand, India

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Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscripts presented as Chapters 7 and 8 within this thesis, for which I am a co-author, are substantially the work of the first author, Eden Cottee-Jones. My role has been limited to identifying the plants recorded in Assam and commenting on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

Omesh Bajpai

22nd September 2014



राष्ट्रीय वनस्पति अनुसंधान संस्थान

(वैज्ञानिक एवं औद्योगिक अनुसंधान परिषद्)

राणा प्रताप मार्ग, पोस्ट बाक्स सं० 436, लखनऊ-226 001 (भारत)

NATIONAL BOTANICAL RESEARCH INSTITUTE

(Council of Scientific & Industrial Research)

Rana Pratap Marg, P.B. No. 436, Lucknow-226001 (India)

सं०/No.

दिनांक/Date

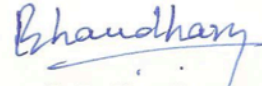
Dr. Lal Babu Chaudhary
Principal Scientist
Plant Diversity, Systematics and Herbarium Division
E-mail: dr_lbchaudhary@rediffmail.com

22 September 2014

Isolated *Ficus* trees and conservation in human-modified landscapes

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(L. B. Chaudhary)

डा० एल० बी० चौधरी
Dr. L. B. Chaudhary
वैज्ञानिक/Scientist
राष्ट्रीय वनस्पति अनुसंधान संस्थान
National Botanical Research Institute
राणा प्रताप मार्ग, लखनऊ-226 001 (भारत)
Rana Pratap Marg, Lucknow-226 001 (India)

EPABX Phones : 205831-35, 205848, 205839, 205899, 207819
E-mail : directornbri@satyam.net.in

Gram : BAGH, Lucknow
Fax : (0522) 205839, 205836
Website :www.nbri-iko.org



Australian
National
University

23 September 2014

Dr Philip Gibbons
Senior Lecturer

Fenner School of Environment & Society
The Australian National University

T +61 2 6125 2562
F +61 2 6125 0746
Philip.Gibbons@anu.edu.au

Building 141, Linnaeus Way
Canberra ACT 2601 Australia
www.anu.edu.au

CRICOS Provider No. 00120C

Isolated *Ficus* trees and conservation in human-modified landscapes

Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscript presented as Chapter 9 within this thesis, for which I am a co-author, is substantially the work of the first author, Eden Cottee-Jones. The model used to simulate *Ficus* population densities in this chapter is one that I developed here at The Australia National University. My role in this manuscript has been to modify and assist Eden with the use of this model, along with commenting on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

Yours sincerely,

A handwritten signature in black ink, appearing to read 'Philip Gibbons'.

DR PHILIP GIBBONS

Dr. Dhanya B.,
Assistant Professor,
School of Development
Phone: +91-9844316406
email:dhanya.b@apu.edu.in



Pixel Park, B Block,
PESIT IT Campus,
Electronics city, Hosur Road
Bangalore-560100
www.azimpremjiuniversity.edu.in

Isolated *Ficus* trees and conservation in human-modified landscapes

Thesis submitted for the degree of Doctor of Philosophy by H. Eden W. Cottee-Jones

I declare that the manuscript presented as Chapter 9 within this thesis, for which I am a co-author, is substantially the work of the first author, Eden Cottee-Jones. My role has been limited to providing data for the *Ficus* age regression models and commenting on drafts. I therefore consent to the inclusion of this material in Eden's doctoral thesis.

A handwritten signature in black ink, appearing to read "Eden W. Cottee-Jones", written over a light grey rectangular background.

22nd September 2014

APPENDIX 5:

Details of the trees surveyed for this thesis

This appendix contains information concerning the trees surveyed as part of the thesis. The trees are listed by category in the first instance, starting with *Ficus*, and followed by fruit trees and then large trees. Within each category, trees are listed by family in alphabetical order. The table presents details of the geographical position of each tree (with co-ordinates provided for latitude and longitude in decimal degrees, WGS84), diameter at breast height (DBH, in metres), height (m), and canopy area (m²), along with the codes used to identify each tree during the data analysis. Please see the Methods (Chapter 3) for details of how each variable was measured.

Category	Species	Family	Code	Location (decimal degrees WGS84)		DBH (m)	Height (m)	Canopy area (m ²)
				Lat	Long			
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_65	26.63095702	93.72836298	1.09	18.72	179.82
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_40	26.65207003	93.63607102	3.14	16.01	351.36
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_553	26.65562103	93.61562898	1.48	22.04	645.04
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_662	26.55311798	93.85617603	0.89	14.70	206.25
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_443	26.59040898	93.926654	2.87	27.78	1742.13
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_233	26.65693598	93.81294603	0.95	26.18	810.25
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_918	26.67121598	93.90078804	1.10	12.74	324.34
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_347	26.58559601	93.86042004	1.55	30.26	160.60
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_815	26.52700198	93.92933403	1.93	29.22	936.21
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_451	26.60160603	93.92542999	1.16	17.39	508.00
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_366	26.61323198	93.824979	0.83	16.71	433.97
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_174	26.63208104	93.76217097	2.87	22.68	512.61
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_54	26.64066402	93.69959	2.54	34.11	1806.42
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_436	26.66092602	93.83524599	0.51	20.58	99.75
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_66	26.63093297	93.72886498	1.61	25.01	412.33
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_828	26.55498002	93.90059902	2.15	33.81	539.12
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_131	26.708036	93.77819097	3.22	41.80	1781.28
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_437	26.660736	93.83431996	0.89	17.70	203.30
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_179	26.62871503	93.76685997	0.69	24.74	166.91
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	E_196	26.61790296	93.80458198	1.27	33.57	888.68
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_297	26.63796321	93.58557215	1.05	22.46	255.73
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_313	26.58773608	93.39030096	2.01	30.57	551.35
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_25	26.63755668	93.58813223	1.85	25.19	664.45
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_285	26.58759585	93.37856471	0.63	19.32	438.96
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_210	26.61076309	93.48947883	1.18	31.54	381.62

<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_203	26.61042145	93.48610494	1.66	37.50	1102.70
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_29	26.63796321	93.58557215	1.05	22.46	255.73
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_317	26.60578843	93.42992842	1.46	42.12	563.60
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_41	26.61211585	93.59469996	1.02	30.74	286.51
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_282	26.58761244	93.37862673	1.15	21.16	301.59
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_198	26.61051013	93.48322995	1.62	36.31	819.33
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_325	26.62852644	93.59594618	1.37	23.57	419.09
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_196	26.61051013	93.48322995	1.62	36.31	819.33
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_377	26.641422	93.57179976	1.27	22.73	565.49
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_71	26.58628433	93.34550539	0.92	33.36	278.78
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_175	26.60589564	93.46494164	0.99	25.59	283.50
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_108	26.66570554	93.61334257	1.46	43.04	737.17
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_399	26.59339688	93.44094836	1.08	26.08	314.16
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_416	26.6108454	93.59384668	1.59	30.75	706.86
<i>Ficus</i>	<i>F. benghalensis</i> L.	Moraceae	M_417	26.67848468	93.61832988	1.26	18.53	271.18
<i>Ficus</i>	<i>F. benjamina</i> L.	Moraceae	M_19	26.59458761	93.44059138	1.02	30.16	138.54
<i>Ficus</i>	<i>F. benjamina</i> L.	Moraceae	M_101	26.60268034	93.40112921	0.54	17.01	249.68
<i>Ficus</i>	<i>F. benjamina</i> L.	Moraceae	M_39	26.62450103	93.58415804	0.99	24.26	526.02
<i>Ficus</i>	<i>F. benjamina</i> L.	Moraceae	M_28	26.63870785	93.58622544	1.02	37.50	381.70
<i>Ficus</i>	<i>F. benjamina</i> L.	Moraceae	M_45	26.61180396	93.60529192	1.40	14.25	240.53
<i>Ficus</i>	<i>F. benjamina</i> L.	Moraceae	E_S18	26.61748907	93.51493115	3.88	42.30	1174.96
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	E_35	26.63848196	93.63483402	1.72	24.32	273.71
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	E_F111	26.60958661	93.50328617	1.90	36.47	667.75
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	M_43	26.59421663	93.45141669	1.40	19.19	439.19
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	M_104	26.63089902	93.53762942	2.45	40.57	687.75
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	M_20	26.60934437	93.50592337	1.85	23.55	530.14
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	M_17	26.60820032	93.50431815	1.66	20.50	549.78
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	M_448	26.59018099	93.41636114	1.91	29.71	801.11
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	M_246	26.61841678	93.5146159	1.40	37.50	467.63
<i>Ficus</i>	<i>F. microcarpa</i> L.f.	Moraceae	E_S58	26.58539501	93.42169957	2.28	37.45	921.47

<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_FN2	26.6369448	93.59125927	1.41	17.34	329.28
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_313	26.59119101	93.44930705	1.75	26.13	443.01
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_171	26.63501998	93.761069	0.73	20.33	229.02
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_89	26.64424402	93.752426	0.69	22.27	327.12
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_328	26.58861098	93.90625102	2.08	31.46	597.28
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_472	26.594511	93.95923899	0.81	13.18	261.25
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_F138	26.58628626	93.34626555	1.19	26.03	424.46
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_F145	26.58626019	93.34645397	0.71	28.16	205.62
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_147	26.58623463	93.34228272	1.72	27.32	551.42
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_309	26.60918528	93.57257769	1.55	30.33	463.49
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_96	26.64479898	93.75928902	1.46	30.85	454.24
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_719	26.50393196	93.91433696	1.16	18.89	230.84
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_245	26.65967602	93.83450202	1.57	28.02	472.46
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_475	26.63853401	93.92667797	1.47	24.43	534.22
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_157	26.64022699	93.760119	1.26	22.40	391.46
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_395	26.62792403	93.92546201	0.87	17.62	342.90
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_827	26.55482504	93.90073003	1.75	25.01	426.26
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_133	26.70786501	93.77824796	2.44	51.70	1347.74
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_537	26.64994396	93.66797699	1.59	25.02	269.88
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_534	26.65837398	93.66606298	1.50	25.84	359.04
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_435	26.66098301	93.83551296	0.95	16.96	213.75
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_353	26.60096297	93.84325398	1.26	29.58	353.96
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_67	26.63094596	93.72911601	0.42	26.40	210.42
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_535	26.65630599	93.66577003	1.64	29.23	683.30
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_189	26.619808	93.79350998	1.35	31.70	399.36
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_225	26.64330902	93.78037202	1.09	18.27	156.39
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_226	26.64337498	93.78057604	0.64	18.96	71.53
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_194	26.61901399	93.80162903	0.95	23.91	300.65
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_522	26.67062799	93.68051296	1.25	49.88	143.14
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_195	26.61821603	93.80401201	0.52	19.70	133.74

<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_527	26.669954	93.67877497	1.39	40.25	283.53
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	E_526	26.67009397	93.67907203	0.99	26.55	377.63
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_73	26.58628433	93.34550539	0.92	33.36	278.78
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_291	26.61075261	93.48757781	0.83	25.59	275.88
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_6	26.59634781	93.45836721	1.27	37.59	666.10
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_209	26.61075261	93.48757781	0.83	25.59	275.88
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_261	26.58465673	93.35996392	2.55	26.77	711.57
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_69	26.58637544	93.34236687	1.91	28.61	496.21
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_170	26.60256567	93.45882721	1.18	31.54	490.09
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_121	26.61136718	93.49358755	1.27	37.45	334.89
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_192	26.61057894	93.48220509	1.59	37.50	607.90
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_327	26.59102798	93.41910085	1.08	20.49	290.99
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_326	26.64792962	93.60689571	0.95	18.53	552.68
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_106	26.66666519	93.61389494	1.27	18.53	332.22
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_165	26.60045142	93.4548619	0.70	18.53	233.26
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_156	26.6405616	93.56738158	1.31	21.28	416.26
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_237	26.61677434	93.51129063	1.27	37.50	431.87
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_178	26.60638883	93.4657624	0.76	27.35	309.45
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_148	26.63573571	93.51869898	0.92	18.48	204.83
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_154	26.59563686	93.4451399	1.24	26.18	298.45
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_179	26.60625698	93.46624847	0.99	19.76	185.83
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_398	26.60183854	93.40816506	0.68	19.72	827.81
<i>Ficus</i>	<i>F. religiosa</i> L.	Moraceae	M_60	26.60577133	93.61029793	1.15	21.06	253.68
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_431	26.66194601	93.84190902	1.23	27.89	357.39
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_410	26.63413804	93.90438102	1.67	24.31	503.42
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_414	26.63590302	93.900566	0.59	16.28	116.61
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_832	26.56387297	93.88900098	2.13	29.47	424.59
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_325	26.60158097	93.89635803	1.34	24.21	419.03
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_70	26.63219	93.73457498	3.33	25.31	836.21
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_430	26.66146296	93.84724402	1.42	20.35	160.87

<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	E_213	26.64591696	93.78777903	0.74	19.71	135.91
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	M_342	26.63288277	93.54953282	1.66	35.02	635.54
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	M_182	26.60728586	93.46985671	3.47	19.07	1563.57
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	M_42	26.6124269	93.60263846	2.04	40.15	228.32
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	M_161	26.59970703	93.45281186	2.07	27.64	518.74
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	M_81	26.58581503	93.34603127	1.10	19.61	337.25
<i>Ficus</i>	<i>F. rumphii</i> Blume	Moraceae	M_86	26.5850418	93.34702947	1.27	18.79	354.56
Fruit	<i>Gmelina arborea</i> Roxb.	Lamiaceae	FR_32	26.58698204	93.44560702	0.55	18.52	83.32
Fruit	<i>Premna bengalensis</i> C.B.Clarke	Lamiaceae	FR_23	26.50069403	93.91	0.41	25.78	110.27
Fruit	<i>P. bengalensis</i> C.B.Clarke	Lamiaceae	FR_28	26.52473903	93.93717203	0.44	17.06	69.13
Fruit	<i>Tectona grandis</i> L.f.	Lamiaceae	FR_5	26.59198998	93.39994401	0.49	24.36	28.31
Fruit	<i>T. grandis</i> L.f.	Lamiaceae	FR_12	26.47708196	93.91816297	0.42	23.01	194.26
Fruit	<i>T. grandis</i> L.f.	Lamiaceae	FR_13	26.47755696	93.91798301	0.35	17.32	63.49
Fruit	<i>T. grandis</i> L.f.	Lamiaceae	FR_16	26.47867301	93.92776603	0.52	17.09	60.54
Fruit	<i>T. grandis</i> L.f.	Lamiaceae	FR_17	26.478684	93.92776896	0.42	13.57	111.06
Fruit	<i>T. grandis</i> L.f.	Lamiaceae	FR_19	26.48845503	93.923404	0.40	18.69	122.99
Fruit	<i>Dysoxylum binectariferum</i> Hook f. ex. Bedd.	Meliaceae	FR_9	26.48091299	93.91867602	0.14	16.34	25.87
Fruit	<i>D. binectariferum</i> Hook f. ex. Bedd.	Meliaceae	FR_10	26.478067	93.92139704	0.17	18.45	37.84
Fruit	<i>Toona ciliata</i> M.Roem.	Meliaceae	FR_7	26.59376401	93.39779103	0.50	24.23	87.18
Fruit	<i>T. ciliata</i> M.Roem.	Meliaceae	FR_8	26.491858	93.91349701	0.37	20.76	35.63
Fruit	<i>Artocarpus heterophyllus</i> Lam.	Moraceae	FR_11	26.59536604	93.452319	0.38	15.04	37.96
Fruit	<i>A. heterophyllus</i> Lam.	Moraceae	FR_18	26.48155304	93.92688702	0.36	8.97	47.17
Fruit	<i>A. heterophyllus</i> Lam.	Moraceae	FR_20	26.49025898	93.92290402	0.48	10.48	52.87
Fruit	<i>A. heterophyllus</i> Lam.	Moraceae	FR_21	26.49018698	93.92282196	0.50	14.33	67.58
Fruit	<i>A. heterophyllus</i> Lam.	Moraceae	FR_31	26.63106498	93.83549301	0.52	15.44	49.50
Fruit	<i>A. heterophyllus</i> Lam.	Moraceae	FR_33	26.63088896	93.83539896	0.49	17.48	57.39
Fruit	<i>Artocarpus lakoocha</i> Roxb.	Moraceae	FR_2	26.60526196	93.42740698	0.50	27.59	43.29

Fruit	<i>A. lakoocha</i> Roxb.	Moraceae	FR_3	26.58644803	93.35365897	0.52	28.03	57.39
Fruit	<i>A. lakoocha</i> Roxb.	Moraceae	FR_15	26.46999699	93.92784004	0.46	19.43	40.29
Fruit	<i>A. lakoocha</i> Roxb.	Moraceae	FR_29	26.527811	93.92835301	0.53	26.39	74.38
Fruit	<i>Syzygium cumini</i> (L.) Skeels	Myrtaceae	FR_24	26.50063	93.91014299	0.50	22.25	124.91
Fruit	<i>S. cumini</i> (L.) Skeels	Myrtaceae	FR_25	26.49882898	93.90534201	0.39	12.85	87.38
Fruit	<i>S. cumini</i> (L.) Skeels	Myrtaceae	FR_26	26.49915403	93.89660203	0.46	20.39	109.30
Fruit	<i>S. cumini</i> (L.) Skeels	Myrtaceae	FR_27	26.52201802	93.93926801	0.63	26.98	152.39
Fruit	<i>Phyllanthus emblica</i> L.	Phyllanthaceae	FR_6	26.59233799	93.39832303	0.32	11.37	29.49
Fruit	<i>P. emblica</i> L.	Phyllanthaceae	FR_14	26.47393104	93.92441796	0.53	23.54	92.29
Fruit	<i>Carallia brachiata</i> (Lour.) Merr.	Rhizophoraceae	FR_1	26.59461804	93.45157804	0.32	12.78	42.38
Fruit	<i>C. brachiata</i> (Lour.) Merr.	Rhizophoraceae	FR_4	26.58757296	93.37791796	0.28	10.12	36.89
Fruit	<i>Neolamarckia cadamba</i> (Roxb.) Bosser	Rubiaceae	FR_22	26.59500503	93.45257004	0.95	31.49	151.19
Fruit	<i>Citrus maxima</i> (Burm.) Osbeck	Rutaceae	FR_30	26.659542	93.82775098	0.39	12.39	58.39
Large	<i>Mangifera indica</i> L.	Anacardiaceae	R_1	26.62494502	93.84167902	0.63	18.71	148.25
Large	<i>M. indica</i> L.	Anacardiaceae	R_2	26.62431898	93.84273497	0.57	18.36	71.30
Large	<i>M. indica</i> L.	Anacardiaceae	R_28	26.59553099	93.44488048	0.40	15.86	95.57
Large	<i>Mesua ferrea</i> L.	Calophyllaceae	R_29	26.59525272	93.45168122	0.37	14.01	61.28
Large	<i>Terminalia catappa</i> L.	Combretaceae	R_27	26.59227102	93.45036099	0.80	30.51	539.06
Large	<i>P. bengalensis</i> C.B.Clarke	Lamiaceae	R_31	26.64137573	93.57381301	0.60	19.13	97.49
Large	<i>T. grandis</i> L.f.	Lamiaceae	R_10	26.65715399	93.81437598	0.41	20.39	93.49
Large	<i>T. grandis</i> L.f.	Lamiaceae	R_21	26.66354796	93.79787302	0.64	27.39	69.39
Large	<i>Bombax ceiba</i> L.	Malvaceae	R_26	26.59173198	93.44772203	1.69	21.18	427.16
Large	<i>Chickrassia tabularis</i> Wight & Arn.	Meliaceae	R_14	26.65877396	93.81366402	0.68	21.94	277.39
Large	<i>C. tabularis</i> Wight & Arn.	Meliaceae	R_18	26.653143	93.80653001	0.75	25.39	129.49
Large	<i>T. ciliata</i> M.Roem.	Meliaceae	R_25	26.67612199	93.79040298	1.09	32.39	321.20
Large	<i>Albizia lucidior</i> (Steud.) I.C.Nielsen	Mimosaceae	R_7	26.65677303	93.81424103	0.38	15.54	144.98

Large	<i>A. lucidior</i> (Steud.) I.C.Nielsen	Mimosaceae	R_16	26.65268904	93.806772	0.39	25.00	67.73
Large	<i>A. lucidior</i> (Steud.) I.C.Nielsen	Mimosaceae	R_20	26.58091798	93.455166	0.44	23.50	74.19
Large	<i>Albizia procera</i> (Roxb.) Benth.	Mimosaceae	R_6	26.65688502	93.81425201	0.52	17.20	44.15
Large	<i>A. procera</i> (Roxb.) Benth.	Mimosaceae	R_8	26.656796	93.81444404	0.69	13.43	44.67
Large	<i>A. procera</i> (Roxb.) Benth.	Mimosaceae	R_9	26.58616698	93.45123698	0.48	17.20	44.15
Large	<i>Albizia saman</i> (Jacq.) Merr.	Mimosaceae	R_3	26.617032	93.80644402	0.62	19.09	232.52
Large	<i>A. saman</i> (Jacq.) Merr.	Mimosaceae	R_17	26.65264796	93.80673101	0.62	19.09	232.52
Large	<i>A. saman</i> (Jacq.) Merr.	Mimosaceae	R_24	26.67633899	93.79038303	0.63	25.38	155.01
Large	<i>A. lakoocha</i> Roxb.	Moraceae	R_19	26.65417397	93.80539703	0.69	29.39	80.38
Large	<i>S. cumini</i> (L.) Skeels	Myrtaceae	R_11	26.65795203	93.81361096	0.40	14.20	92.36
Large	<i>S. cumini</i> (L.) Skeels	Myrtaceae	R_13	26.65830499	93.81347802	0.64	19.38	99.49
Large	<i>S. cumini</i> (L.) Skeels	Myrtaceae	R_15	26.65272298	93.80686001	1.05	18.36	79.00
Large	<i>S. cumini</i> (L.) Skeels	Myrtaceae	R_22	26.67636498	93.790464	0.35	19.30	59.50
Large	<i>S. cumini</i> (L.) Skeels	Myrtaceae	R_23	26.67630002	93.79021397	0.50	21.50	46.50
Large	<i>Neolamarckia cadamba</i> (Roxb.) Bosser	Rubiaceae	R_4	26.658191	93.818478	0.53	26.34	38.45
Large	<i>N. cadamba</i> (Roxb.) Bosser	Rubiaceae	R_5	26.65733504	93.81452199	0.53	23.89	18.73
Large	<i>N. cadamba</i> (Roxb.) Bosser	Rubiaceae	R_12	26.65804499	93.81354298	0.40	17.57	85.05
Large	<i>Palaquium polyanthum</i> (Wall. ex G.Don) Baill.	Sapotaceae	R_30	26.63812146	93.56196536	0.51	17.49	62.82