1 **Title:** Factors affecting the survival of tree seedlings following shifting cultivation in the Eastern
2 Himalaya

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32 **Running headline:** Seedling survival in a swidden landscape

33 Abstract

34 1. The seedling stage is considered an important bottleneck determining forest community
35 composition during succession. Seedling growth and survival are known to be affected by factors
36 such as light availability, herbivory and competition with existing vegetation. A shifting cultivation
37 landscape with a cycle of clearing and regeneration provides an experimental setup to understand
38 secondary succession.

39 2. We introduced tree seedlings of three species with differing life history strategies in an uncut
40 forest and in sites formed 2, 6, 12, 25, 50 and 100 years following shifting cultivation in a
41 subtropical landscape in the Eastern Himalaya. Seedlings of a pioneer species *Saurauia nepalensis*,
42 a mid-successional species *Terminalia myriocarpa* and a mature forest species *Castanopsis indica*
43 were introduced in plots with a control and three treatments: shading (light manipulated), clearing
44 of vegetation (reduced competition), and exclosures (mammal herbivory excluded) and monitored
45 for 18, 22 and 23 months, respectively.

46 3. *Saurauia* survived relatively well in all sites, *Terminalia* seedlings survived relatively well in the
47 12 and 25 year sites, and *Castanopsis* seedlings survived well in the 100 year site and the uncut
48 forest. In the early successional site, survival of *Saurauia* was higher within exclosures indicating
49 negative effects of herbivory. In the same site, clearing vegetation improved the survival of
50 *Terminalia*, implying competition with existing vegetation. *Castanopsis* had the highest survival in
51 uncut forest and survival was almost nil in the early successional site.

52 4. Synthesis: Seedling survival in a successional landscape depended on species- as well as site-
53 specific factors. The existing vegetation in an early successional site had a negative effect on the
54 survival of the mid-successional species, while herbivory had a negative effect on the pioneer
55 species. Survival of the mature forest species in the early successional site was negligible but was
56 high in old successional and uncut forest sites, indicating that mature forest species can colonize
57 sites and survive only after certain physical and biotic aspects of the environment have been met.

58 Our experiments were useful to examine factors that affect survival of tree species with differing
59 life history strategies in a shifting cultivation landscape.
60 Keywords: Arunachal Pradesh, North-east India, herbivory, light availability, shade, competition.

61 **Introduction**

62 Secondary succession of plants has interested biologists for over a century since Clements (1916)
 63 and Gleason (1917) suggested their contrasting theories: one, a holistic theory with a climax
 64 equilibrium stage and the other an individualistic one with an open-ended view of succession. Egler
 65 (1954) suggested that vegetation development occurs in one of two ways: relay floristics, in which
 66 one species establishment relays to the next and initial floristics, in which different species establish
 67 in a site and assume predominance at different stages of development. In terms of the processes
 68 during succession, Connell and Slatyer (1977) suggested three distinct mechanisms of species
 69 interactions: facilitation, tolerance and inhibition, while Pickett, Collins and Armesto (1987)
 70 suggested a combination of these at different successional stages. More recent research has focussed
 71 on additional factors that affect successional patterns such as: 1) the disturbance regime; the scale
 72 and frequency of disturbances (Denslow, 1980; Lawrence et al., 2005), 2) environmental factors
 73 such as soil and climate (Bazzaz, 1979; Pickett, Collins & Armesto, 1987), 3) biotic factors such as
 74 herbivory (Coley, 1983), phylogenetic structure of plant communities (Letcher et al. 2014), life
 75 history strategies (Bazzaz, 1979; Denslow, 1980) and functional traits of species (Schleicher,
 76 Peppler-Lisbach & Kleyer 2011).

77
 78 These factors can be expected to be species- and site-specific in different seral stages of succession
 79 (Bazzaz, 1979; Uhl, 1987). Initially, during succession from a clearing to a forest, early
 80 successional species may establish and survive since they are better adapted to the harsh and
 81 variable environmental conditions, whereas propagules of mature forest species and old
 82 successional species may fail to germinate and survive in such sites (Bazzaz, 1979). Among the
 83 environmental factors that affect species differentially, light availability has been shown to limit
 84 tree seedling recruitment of some species while facilitating that of others (Beckage, Lavine & Clark,
 85 2005; Walters & Reich, 1996). Herbivory by vertebrate browsers and invertebrates, which is
 86 considered an important bottleneck in the regeneration stage, can also be expected to vary in

87 different successional stages (De Steven, 1991; Coley & Barone, 1996). Insect herbivory has been
 88 shown to be high during the early years of succession, with herbivory assemblages changing from
 89 foliar-feeding insects in early stages to sap-feeding insects in the later stages of succession (Brown
 90 & Gange, 1992, Carson & Root, 1999). While mammal herbivory can be higher in early
 91 successional sites due to higher visibility of seedlings, it can also be higher in older successional
 92 sites and forests where the vertebrate abundance is usually higher (Tabarelli & Peres, 2002).
 93 Existing vegetation in an early successional site may foster survival of pioneer species while
 94 hindering that of mature forest species (Davis, Wragge & Reich, 1998; Putz & Canham, 1992).
 95
 96 These theories pertaining to succession mechanisms and the role of biotic and abiotic factors can be
 97 tested by introducing propagules of species with different life history strategies in mature forest and
 98 different-aged successional sites, manipulating different factors in plots within sites and monitoring
 99 their survival over time. Several studies in the past have undertaken such experiments (*e.g.* Armesto
 100 & Pickett, 1985; Beckage & Clark, 2003; Berkowitz, Charles & Victoria, 1995; De Steven, 1991;
 101 Uhl, 1987), however field experiments from the Old World are few (Fayolle et al., 2015, Goodale et
 102 al., 2014; Khan & Tripathi, 1989, Lin et al., 2014). These multi-factor experiments are difficult to
 103 simulate in natural conditions. However, a shifting cultivation landscape, which involves a
 104 continuous cycle of clearing and secondary succession, creating a landscape where spatially
 105 separated sites can represent temporal stages of succession, provides such a quasi-experimental
 106 setup. The succession phase, however, is relatively short due to repeated cycles of cultivation and
 107 site manipulation for cultivation can alter natural succession patterns. Despite these shortcomings,
 108 studying succession at such sites has practical advantages: while patterns in older sites can be used
 109 to infer succession over relatively long periods of time, successional sites representing a range of
 110 different-aged sites can be used to identify temporal trends in succession (Pickett, 1989).
 111
 112 We used an artificially maintained seral stage gradient (from recently cleared to mature forest) to
 113 measure seedling success of three tree species with contrasting life history traits. We chose a

114 pioneer, an intermediate and a mature forest species based on the relative abundances of the species
 115 in different successional sites and uncut forest in the study site (data from Teegalapalli & Datta
 116 2016). We undertook a series of controlled experiments to examine the effects of light availability,
 117 herbivory and competition on survival across this gradient. The specific objectives of our research
 118 were: 1) to understand the effects of the age of a successional site on the seedling survival of a
 119 mature, a pioneer and a mid-successional tree species, and 2) to understand the effects of shade,
 120 existing vegetation and mammalian herbivory on the seedling survival of these species in different-
 121 aged successional sites and uncut forest. Based on existing literature, we predicted that: 1) the three
 122 species will have higher seedling survival in the successional sites where the adults of the species
 123 were relatively abundant, 2) herbivory by mammals will negatively affect seedling survival in the
 124 early successional site, 3) providing artificial shade will improve seedling survival, particularly for
 125 the mature species in the early successional sites, and, 4) clearing aboveground vegetation in the
 126 early successional sites will improve seedling survival of the three species by reducing competition.

127

128 **Materials and methods**

129 *Study site*

130 We undertook our experiments in a shifting cultivation landscape around Bomdo village in the
 131 Eastern Himalaya (Figure 1). The village is located in the Upper Siang district of the state of
 132 Arunachal Pradesh (India) at 28.753° N and 94.896° E. The region receives relatively high rainfall
 133 of over 4000 mm every year (Anonymous, 2015) and features tropical wet- and semi-evergreen
 134 forests and sub-tropical broad-leaved forests in the areas above 800 msl (Singh et al., 1996). The
 135 resident *Adi* community practice shifting cultivation in a rotational system in three large blocks
 136 around the village. The fallow period, the gap between two cultivation cycles is at least 10 years, as
 137 shown in other sites in the Upper Siang district (Borang, 1997). Some of the patches in the
 138 landscape have been abandoned for relatively long periods (over 100 years) due to factors such as
 139 inaccessibility and low productivity. The *Adi* maintain a systematic oral cultivation history based on

140 which we selected successional sites that were cultivated and left fallow for 2, 6, 12, 25, 50 and
 141 about 100 years and an uncut forest site (hereafter, referred to as uncut forest) in the landscape for
 142 comparison. Uncut forest in this study represents moderately disturbed uncut forest rather than a
 143 mature forest that is devoid of any human disturbance. Hereafter, we refer to the 2 and 6 year sites
 144 as early, the 12 and 25 year sites as intermediate and the 50 and 100 year old sites as old
 145 successional sites. The sites were located within 1000 m distance of each other and ranged in
 146 elevation from 750 to 1100 msl. Prior permission to undertake the research in the shifting
 147 cultivation landscape around the village was sought from the village elders.
 148

149 **Figure 1:** Map depicting the location of the study area in the Arunachal Pradesh state in north-east
 150 India. The manipulative experiments to understand factors that affect tree seedling survival were
 151 undertaken in the shifting cultivation landscape around the Bomdo village.
 152

153 *Study species*

154 We used three species with differing life-history strategies: *Castanopsis indica* (Roxb.) A. DC.
 155 (Family Fagaceae), *Saurauia nepalensis* Wall. (Family Actinidiaceae) and *Terminalia myriocarpa*

156 Van Huerck et Muell.-Arg. (Family Combretaceae) for the experiments. These species were
 157 selected based on vegetation data collected from 2, 12, 25 and 50 year sites and uncut forest, for
 158 another study (Teegalapalli & Datta, 2016). *C. indica*, (hereafter, *Castanopsis*) is a shade-tolerant
 159 mature forest species that was recorded only from the uncut forest and comprised about 6 % of all
 160 individuals in that forest. *C. indica* and two more species from the genus *Castanopsis* comprised
 161 about a fourth of all individuals recorded from the uncut forest. *S. nepalensis*, (hereafter, *Saurauia*),
 162 a light-loving pioneer species was a dominant species in the early successional sites comprising 70
 163 % and 44 % of all trees recorded from 6 and 12 year old sites, and was not recorded from the 100
 164 year site and uncut forest. *T. myriocarpa*, (hereafter, *Terminalia*), a fast-growing hardwood species
 165 (Bhattacharya & Nanda, 2005; Qureshi, 1968) was recorded in low numbers, only from
 166 intermediate successional sites (12 and 25 year sites), and is considered as a mid-successional
 167 species. While in this site it was only recorded from intermediate successional stages, the species
 168 has been recorded as a dominant tree in tropical semi-deciduous forests in Arunachal Pradesh and
 169 other parts of North-east India (Bhuyan, Khan & Tripathi et al., 2003).

170

171 *Experimental setup*

172 We used a multifactorial design with three treatments within each block: clearing of above-ground
 173 vegetation to reduce competition with existing vegetation, artificial shade to manipulate available
 174 light and exclusion of mammal herbivory across different-aged sites and uncut forest. Although
 175 insect herbivory is an important factor affecting seedling survival in tropical forests (Coley &
 176 Barone, 1996; Crawley, 1983), we did not test for this factor because we refrained from spraying
 177 chemicals to exclude insect herbivory in a shifting cultivation site that was actively used for
 178 agriculture by the local community. We used a block design with eight $1 \times 1 \text{ m}^2$ plots (seven plots
 179 for three treatments, singly and in combination, and a control plot) within each $2 \times 4 \text{ m}^2$ block
 180 (Figure 2). For *Castanopsis* and *Saurauia*, we had three replicates of the blocks and for *Terminalia*
 181 we had five replicates each in the 2, 6, 12, 25, 50, 100 year sites and the uncut forest site.

182 **Figure 2:** The multi-factorial block design depicting shaded plots (grey), vegetation cleared plots in
 183 which above-ground vegetation was cleared quarterly (bottom four plots) and plots with exclosures
 184 (dotted lines). Seedlings were introduced in each of the 1 x 1 m plots nested within the 2 x 4 block.
 185

186 In the treatment plots, we controlled for mammal herbivory by fencing the plot using metal wire-
 187 mesh exclosures. The primary mammalian herbivores in the study area are barking deer (*Muntiacus*
 188 *muntjak*) and wild pig (*Sus scrofa*). Apart from wild mammalian herbivores present in the
 189 landscape, the *Adi* community rears domestic pigs and a species of bovid locally called *Mithun* (*Bos*
 190 *frontalis*), which are free-ranging livestock. We manipulated available light using 40 % artificial
 191 greenhouse shade-netting (leaf litter collected in the net was cleared monthly) and regularly cleared

191 above-ground vegetation (once every three months) to eliminate competition with above-ground
192 vegetation.

193

194 First year seedlings (5–10 cm height) of the three species chosen for the experiments were collected
195 from regenerating secondary and uncut forests in the landscape and planted in the growing season
196 (between March and June) in the different-aged successional sites and uncut forest. We avoided
197 disturbing the roots of the seedlings to prevent root-shock and planted the seedlings within two
198 hours of collection from secondary forests. Overall, for *Castanopsis* and *Saurauia*, we transplanted
199 5 seedlings per $1 \times 1 \text{ m}^2$ plot, 40 seedlings in each block, 120 seedlings in each successional site and
200 the uncut forest, a total of 840 seedlings each across the study site. For *Terminalia*, which had five
201 replicates in each site, we transplanted a total of 1400 seedlings. Based on the availability of the
202 different species of seedlings from natural regeneration, *Castanopsis* seedlings were transplanted in
203 April 2011, *Saurauia* seedlings were transplanted in May 2011 and seedlings were monitored till
204 February 2013. *Terminalia* seedlings were transplanted in July 2012 and monitored till November
205 2013. Seedling survival was monitored monthly and recorded as alive or dead for a period of 23, 22
206 and 18 months for *Castanopsis*, *Saurauia* and *Terminalia*, respectively.

207

208 *Analytical methods*

209 Across all sites

210 Generalized Linear Mixed Models (GLMMs) were used with the proportion of seedlings alive at the
211 end of the study in each $1 \times 1 \text{ m}$ plot as the response variable (varying from 0 to 1). Fixed effects
212 were of the different treatments (singly and in combination) and age of site, and within-site block
213 identity was included as a random effect. To use 'age of the site' as a continuous variable for the
214 analysis, the uncut forest was assigned an age of 300 years (*e.g.* Raman, Rawat & Johnsingh, 1998;
215 Riswan, Kenworthy & Kartawinata, 1985).

216

217 Within a site

218 We used GLMMs with the seedling survival status of each seedling at the end of the study (dead or
219 alive) as the response variable, the different treatments, singly and in combination as fixed effects
220 and variation between blocks as well as variation between seedling replicates as random effects to
221 investigate the importance of treatments within different-aged sites and uncut forest. We used the
222 statistical software R for the analyses with the 'survival' package for survival analysis (Therneau,
223 2015) and 'lme4' package (Bates et al., 2015) for GLMMs (R Development Core Team, 2015).

224

225 Survival curves

226 We used Kaplan-Meier (K-M) survival curves for plotting seedling survival patterns (Kaplan &
227 Meier, 1958). The curves were used to visualise the right-censored survival data (some of the
228 seedlings were still alive at the end of the study) of seedlings in control and treatment plots and log
229 rank tests were used to determine if the curves differed statistically, which indicated the effects of
230 different treatments on the survival period of seedlings. Log rank tests are similar to the Chi-square
231 tests, in which a test statistic is calculated to test the null hypothesis that the survival curves are
232 similar for the groups being compared.

233

234 **Results**

235 *General patterns*

236 Across all sites, overall seedling mortality was 7 %, 23 % and 35 % within the first month for
237 *Saurauia*, *Castanopsis* and *Terminalia*, respectively, which increased to 25 %, 30 % and 55 % in
238 the first three months. A majority of the mortality in the first quarter was from the early
239 successional sites. About a third of the seedlings of *Castanopsis* and *Saurauia* and about a fourth of
240 the seedlings of *Terminalia* survived till the end of the study. While few *Saurauia* seedlings
241 survived in the control plots in the 2 year site (13 % survival), seedlings in the control plots
242 survived relatively well in the 6 (40 % survival) and 12 year (33 % survival) sites as well as in the
243 100 year site (47 %) and the uncut forest (33 %, Figure 3). The survival of *Castanopsis* was very

Figure 3: Overall survival of *Saurauia nepalensis* (N=105), *Castanopsis indica* (N=105) seedlings over a period of 21 months and *Terminalia myriocarpa* (N=175) seedlings in the control plots over a period of 18 months, averaged across different ages.

Seedling survival across all sites

The output of the GLMM undertaken across sites with the age of site and different treatments as predictor variables and proportion of seedlings alive at the end of the study as the response variable indicated that while the age of site did not have a significant effect on *Saurauia* and *Terminalia* seedling survival, survival of *Castanopsis* increased with age ($F = 0.01$, $p = 0.005$, Figure 4, Table 1, full model results in Table S1 – S3). Across all sites, survival of *Saurauia* was higher in exclosure plots ($F = 1.83$, $p = 0.01$, Table 1). None of the treatments had a significant effect on the survival of *Terminalia*.

Figure 4: Survival of *Saurauia nepalensis* (n=105), *Castanopsis indica* (n=105) and *Terminalia myriocarpa* (n=175) in the control plots in successional sites formed following 2, 6, 12, 25, 50 and 100 years following shifting cultivation. The uncut forest site has been assigned an age of 300 years to show the survival of the three species in the site.

Table 1: Generalised Linear Mixed Models results for seedling survival of *Castanopsis indica*, *Saurauia nepalensis* and *Terminalia myriocarpa* seedlings (pooled across each 1 × 1 m plot) at the end of the study across successional sites formed 2, 6, 12, 25, 50 and 100 years following shifting cultivation and uncut forest and treatments (* indicates a *p*-value < 0.05). Proportion of seedlings alive at the end of the study was the response variable. The factors examined were shade, herbivory and competition with aboveground vegetation. Greenhouse shade netting was used to manipulate available light, exclosures were used to prevent herbivory by mammals and vegetation was cleared to eliminate competition with existing vegetation. Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests for parameters are shown.

<i>Castanopsis indica</i> across all sites and treatments				
	Estimate	S.E.	z value	<i>p</i>
Age	0.01	0.004	2.8	0.005**
<i>Saurauia nepalensis</i> across all sites and treatments				
Exclosures - herbivory	1.81	0.72	2.52	0.01**
<i>Terminalia myriocarpa</i> across all sites and treatments				
No effects of age or treatment on seedling survival				

Seedling survival within sites

GLMM analysis undertaken in different-aged sites and uncut forest indicated factors that affected seedling survival specifically in each site. For *Saurauia* in the 2 year site, exclosure plots singly ($F = 2.39, p = 0.02$) and in combination with shade ($F = 2.10, p = 0.03$) had significantly higher seedling survival in comparison with control plots (Table 2). Exclosure plots in uncut forest ($F = 2.91, p = 0.00$) also had higher seedling survival than control plots (Table 2).

Table 2: Generalised Linear Mixed Models results for seedling survival of *Saurauia nepalensis* seedlings (pooled across each 1×1 m plot) at the end of the study within successional sites formed 2, 6, 12, 25, 50 and 100 years following shifting cultivation and uncut forest (only sites where specific factors had a significant effect on seedling survival have been shown, * indicates a p -value < 0.05). The factors examined were shade, herbivory and competition with aboveground vegetation. Greenhouse shade netting was used to manipulate available light, exclosures were used to prevent herbivory by mammals and vegetation was cleared to eliminate competition with existing vegetation. Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests for parameters are shown.

<i>Saurauia nepalensis</i> in 2 year site				
	Estimate	S.E.	z value	p
Intercept	-1.96	0.83	-2.35	0.02*
Exclosures	2.39	1.04	2.29	0.02*
Shade + Exclosures	2.10	1.04	2.03	0.04*
<i>Saurauia nepalensis</i> in uncut forest site				
Exclosures	2.91	1.00	2.90	0.004*

For *Terminalia*, vegetation cleared plots ($F = 1.42, p = 0.04$) and plots with all three treatments ($F = 1.78, p = 0.01$) had higher seedling survival than control plots in the 2 year site (Table 3). For *Terminalia*, there were unexpected results with the treatments in the 12 year site; shade and vegetation cleared plots had lower survival than control plots ($F = -1.54, p = 0.02$, Table 3).

Table 3: Generalised Linear Mixed Models results for survival of *Terminalia myriocarpa* seedlings (pooled across each 1×1 m plot) at the end of the study within successional sites formed 2, 6, 12, 25, 50 and 100 years following shifting cultivation and uncut forest (only sites where specific factors had a significant effect on seedling survival have been shown, * indicates a p -value < 0.05). The factors examined were shade, herbivory and competition with aboveground vegetation. Greenhouse shade netting was used to manipulate available light, exclosures were used to prevent herbivory by mammals and vegetation was cleared to eliminate competition with existing vegetation. Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests for parameters are shown.

<i>Terminalia myriocarpa</i> in 2 year site				
	Estimate	S.E.	z value	<i>p</i>
Intercept	-0.99	0.50	-1.97	0.05*
Vegetation cleared	1.42	0.69	2.06	0.04*
Shade + Exclosures + Vegetation cleared	1.78	0.70	2.53	0.01*
<i>Terminalia myriocarpa</i> in 12 year site				
Shade + Vegetation cleared	-1.54	0.65	-2.37	0.02*

344

345 For *Castanopsis*, in the 25 year site, shade, singly ($F = 3.00$, $p = 0.00$) and in combination with
 346 exclosures ($F = 2.23$, $p = 0.03$) as well as in combination with all treatments ($F = 3.85$, $p = 0.00$)
 347 had higher survival than control plots (Table 4).

348

349 **Table 4:** Generalised Linear Mixed Models results for survival of *Castanopsis indica* seedlings
 350 (pooled across each 1×1 m plot) at the end of the study within successional sites formed 2, 6, 12,
 351 25, 50 and 100 years following shifting cultivation and uncut forest (only sites where specific
 352 factors had a significant effect on seedling survival have been shown, * indicates a p -value < 0.05).
 353 The factors examined were shade, herbivory and competition with aboveground vegetation.
 354 Greenhouse shade netting was used to manipulate available light, exclosures were used to prevent
 355 herbivory by mammals and vegetation was cleared to eliminate competition with existing
 356 vegetation. Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests
 357 for parameters are shown.

358

<i>Castanopsis indica</i> in 25 year site				
	Estimate	S.E.	z value	<i>p</i>
Intercept	-2.45	1.15	-2.12	0.03*
Shade	3.00	1.06	2.82	0.00*
Shade + Exclosures	2.23	1.03	2.15	0.03*
Shade + Exclosures + Vegetation cleared	3.85	1.12	3.43	0.00*

359

360 *Survival curves*

361 The Kaplan-Meier (K-M) survival curves indicated species-specific as well as treatment-specific
 362 differences, which were tested using the log-rank tests, based on which statistically significant
 363 differences ($p < 0.05$) between seedling survival in control and treatments plots were identified
 364 (Figures S1 – S3, Tables S4 – S6). All other survival curves that were not significant have not been
 365 shown.

366

367 For the pioneer species *Saurauia*, survival curves in the herbivory exclosure plots in the 2 and 25
368 year sites and uncut forest were significantly different from those in control plots, respectively
369 (Figure S1). Seedling survival curves of plots with all three treatments combined were significantly
370 different in the 2 year and 50 year site than those in control plots for *Saurauia*. Survival curves in
371 vegetation cleared and control plots the 6 year site were significantly different. Further, survival
372 curves in treatments with shade and vegetation clearing were different from those in control plots in
373 the 12 year and 100 year sites. In the 50 year site, survival curves were significantly different in
374 exclosure plots with vegetation clearing and shade plots in comparison with those in control plots.

375

376 For *Terminalia*, in the 2 year site, survival curves in vegetation cleared plots and plots with all three
377 treatments combined were significantly different from those in control plots (Figure S2). In the 12
378 year site, the survival curves in the shade and vegetation cleared plots were significantly different
379 from those in control plots. In the 25 year sites and the older successional sites and uncut forest, the
380 survival of seedlings in control and treatments plots was lower than 20 % and survival curves for
381 these sites were not plotted.

382

383 For *Castanopsis*, in the 6 year site, survival curves were significantly different between control
384 plots and plots with exclosures and vegetation cleared and plots with all three treatments (Figure
385 S3). In the 25 year site, survival curves were significantly different between control plots and plots
386 with shade and plots with all three treatments. In the 100 year site, plots in which vegetation was
387 cleared had significantly different survival curves in comparison with control plots.

388

389 **Discussion**

390 *Seedling survival patterns*

391 Overall, more than a quarter of the seedlings introduced in this study survived till the end of the
392 study and seedling mortality was highest in the first six months, with the highest mortality in the

early successional site. Seedlings of the pioneer species *Saurauia* survived generally well in all sites (20 – 35 %) except the 25 year site (~8 %), the mid-successional species *Terminalia* seedlings survived relatively well in the 2 year site (~45 %) and the two intermediate sites (6 year [~39%] and 12 year [~47%] sites), and the mature forest species *Castanopsis* seedlings survived well in the 100 year (~53 %) site and the uncut forest (~66 %).

Several *Castanopsis* species are characteristic of mature sub-tropical forests in the Eastern Himalaya (Sundriyal et al., 1994), therefore we expected the survival of the species to be highest in the uncut forest. However, we did not expect that *Saurauia* seedlings would survive well in the older sites and uncut forest, given that it is known to be a pioneer species. Although *Saurauia* seedlings survived in these sites till the end of the study, it is unlikely that they will survive to the adult stage, since we recorded trees of the species in 12 year and 25 year successional sites and did not find trees or seedlings of the species in the vegetation sampling we undertook in the older successional sites and uncut forest (Teegalapalli & Datta, 2016). Similarly, *Saurauia* trees were recorded from early successional fallows formed following shifting cultivation in Vietnam but were not recorded from adjoining old-growth evergreen broad-leaved forest (Van Do, Osawa & Thang, 2010). We speculate that other mortality factors at later stages (sapling or pole) that we did not monitor in our study may result in the absence of this species in late successional sites. The seedling survival patterns of *Terminalia* reflected the adult tree composition patterns recorded from the site: trees of the species were only recorded from the intermediate (6 and 12 year sites) successional sites (Teegalapalli & Datta, 2016).

Factors affecting seedling survival

The pioneer species *Saurauia* was more susceptible to herbivory: introducing exclosures that prevented herbivory by mammals improved the number of seedlings that survived as well as the survival period across all sites. The 'strategic resource allocation' concept (McCook, 1994) suggests

419 that pioneer species expend more on faster growth than on herbivory defense in contrast with slow-
 420 growing mature forest species that need to defend themselves due to their slower growth and
 421 expend more on secondary metabolites (Coley, 1983; Feeny, 1976). The higher rates of growth
 422 have been attributed to better adaptation to nutrient intake and retention under low soil nutrient
 423 conditions and allocation of high amounts of energy to root production (Uhl, 1987). For example, in
 424 Barro Colorado Island, Panama, pioneer species had six times higher levels of herbivory than
 425 mature forest persistent species (Coley, 1983). In this study site, herbivory is likely an important
 426 factor affecting regeneration since the livestock that the resident *Adi* community rear graze in the
 427 successional fallows. *Saurauia* can be expected to be particularly susceptible to herbivory as the
 428 species has relatively high calorific value and is also used as cattle fodder in Sikkim and Nepal
 429 (Chettri & Sharma, 2008).

430
 431 Survival of the mature forest species *Castanopsis* was enhanced in plots with all three treatments
 432 combined; shade, exclosures and vegetation cleared in the 6 and 25 year sites. Specifically,
 433 providing shade in the 25 year old site improved the survival of the species, while seedlings in the 6
 434 and 12 year sites had relatively low survival both in control and shade plots. This indicates that the
 435 favourable conditions required for this shade-loving species to survive were not met even in shaded
 436 plots that provided 40 % of the ambient light conditions in the intermediate successional sites.
 437 However, *Castanopsis* seedlings surviving better in vegetation cleared plots than in control plots
 438 could be due to factors that were not controlled for in this study.

439
 440 *Terminalia* seedlings survived relatively well in the intermediate sites. *T. myriocarpa* is a fast-
 441 growing, light-tolerant species (Bhattacharya & Nanda, 2005; Deb et al., 2014; Qureshi, 1968) and
 442 relatively less affected by herbivory as shown in this study, which likely fosters its survival in the
 443 intermediate successional sites. In the 2 year old site, however, both clearing vegetation, singly as
 444 well as in combination with shade and herbivory exclosures improved survival of the seedlings,

445 indicating that the species is unable to colonize recently abandoned clearing due to a combination of
446 factors.

447

448 *Insights into succession mechanisms*

449 Pickett, Collins and Armesto (1987) suggested that a combination of mechanisms can be applicable
450 in a successional stage in contrast with the individualistic models of facilitation, tolerance and
451 inhibition suggested by Connell and Slatyer (1977). In our study, seedling survival patterns in
452 different treatments indicated species-specific as well as site-specific interactions between species
453 and the existing vegetation. Introducing exclosures and shade positively affected seedling survival
454 of *Saurauia* in the early successional site indicating that pioneer tree species cannot immediately
455 colonize an open area due to the harsh physical conditions and may need to be facilitated by the
456 pioneer shrubs that colonize the clearings first.

457

458 The vegetation in the 2 year site was dominated by seedlings and saplings of the small tree / shrub
459 species *Maesa indica* and *M. ramentaceae* (Teegalapalli & Datta, 2016). Fruits of these species are
460 small and widely dispersed by smaller frugivorous birds and *Maesa indica* is a forest-gap adapted
461 early-successional species in southern India (Chetana & Ganesh, 2012; Ganesh & Davidar, 2001).
462 These species possibly modify the environment to make it suitable for the early successional tree
463 species to colonize, which indicates facilitation. A similar successional trend was recorded in
464 abandoned fields in the Rio Negro region of the Amazon Basin (Uhl, 1987); grasses and forbs
465 dominated in the first year of succession, followed by a dominance of shrubs and long-lived tree
466 species were recorded only after 5 years.

467

468 In contrast, clearing existing vegetation in the early successional site improved the survival of *T.*
469 *myriocarpa* suggesting competition as the likely mechanism inhibiting its survival. However, it was
470 difficult to clearly tease apart if competition with existing vegetation was the single factor that

471 improved survival of seedlings since seedlings in plots with all three treatments also survived better
 472 than control plots in the early successional site. This is particularly so, since in the 12 year site,
 473 contrary to expectations, the combined effect of providing shade and clearing vegetation reduced
 474 the survival of the species. Survival of the mature forest species *Castanopsis* seedlings in control
 475 and treatment plots in the early successional site was negligible, indicating that mature forest
 476 species can colonize sites, survive and reach the adult stage only after certain conditions of the
 477 physical environment have been met.

478

479 **Site-specific factors that can affect seedling survival**

480 A shifting cultivation landscape such as the one used for this research is one that is in a constant
 481 flux of farming management. While the early successional sites are sites that were recently
 482 cultivated, the intermediate sites are the ones that will be cultivated in the future since the fallow
 483 period, the gap between two cultivation phases, is 10 years in the region (Teegalapalli & Datta
 484 2016, Teegalapalli et al. 2018). However, the older 25 and 50 year sites are sites which were
 485 cultivated once and abandoned subsequently due to low soil fertility and crop productivity.
 486 Therefore, it is likely that seedling survival in these sites do not reflect the seedling survival in a site
 487 that has recovered for 25 to 50 years. On the contrary, the 100 year old site in the landscape chosen
 488 for this research was one which was not abandoned for the same reasons and seedling survival in
 489 this site was comparable with that in uncut forest.

490

491 **Conclusion**

492 To our knowledge, this is the first study in India in which manipulative experiments were
 493 undertaken to investigate the importance of multiple factors that affect seedling survival in a
 494 successional landscape. The mature forest tree species did not survive in the early successional
 495 sites, whereas under certain conditions, the mid-successional and the pioneer species survived
 496 relatively well. The seedling survival of the mature species increased with age and was highest in

uncut forest. Mammalian herbivory was an important factor affecting the pioneer species. Existing vegetation negatively affected the survival of *Terminalia* seedlings in the early successional site indicating competition with existing vegetation and more than half of the seedlings of the species survived in the intermediate successional sites from where adult trees of the species were also recorded. This study provided insights into understanding the relative effects of light availability, herbivory and existing vegetation on the seedling survival of a mature forest, a mid-successional and an early successional tree species in successional sites and uncut forest.

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Authors' contributions

KT, RA, SQ and AD conceived the idea and designed the methodology. KT collected the data in the field with inputs from AD, analysed the data with inputs from SQ and wrote the manuscript with inputs from RA, AD and SQ. All authors contributed to the drafts and gave final approval for publication.

Data accessibility

All the data used in the research presented in the manuscript will be archived in Data Dryad.

523

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