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The nurse-plant effect under the dislodgement stress of landslides

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While the mitigating effects of trees on shallow landslide occurrence are well recognised, the impact of landslides on tree community structure and tree-tree interactions have received much less research attention. The structures of tree communities before and after landslides were compared in a 25-ha subtropical forest plot. Tree-tree interactions were examined by analysing the pre- and post-landslide spatial point patterns of large (DBH ≥ 20 cm) and small (1 cm ≤ DBH < 20 cm) tree cohorts. In landslide scarps, 35 (34%) of 104 large trees and 467 (13%) of 3,072 small trees survived. Large (L) and small (S) tree cohorts were paired together for spatial analyses, including pre-landslide ($_{PL}$) (L_{PL}-S_{PL}), surviving ($_S$) (L_S-S_S), and missing ($_M$) large-small tree paired cohorts (L_M-S_M). We randomly selected trees from the pre-landslide tree cohorts to create two virtual paired cohorts, the $L_{34\%}$-$S_{13\%}$ and $L_{66\%}$-$S_{87\%}$ paired cohorts, whose population sizes were identical to the field-observed L_S-S_S and L_M-S_M paired cohorts respectively, but with random spatial patterns. Post-landslide survival rates of trees increased monotonically with DBH. Large trees dislodged by landslides scarcely reduced small-tree survival. Evidence for this included: (i) the distance from small trees to the nearest large trees of the L_M-S_M paired cohort did not differ significantly from that of the virtual $L_{66\%}$-$S_{87\%}$ paired cohort; (ii) survival rates of small trees near L_M individuals did not differ significantly from those without large trees nearby. Surviving large trees had positive effects on the survival of small trees, indicated by: (i) the distance from small trees to the nearest large trees of the L_S-S_S paired cohort was significantly lower than that of the virtual $L_{34\%}$-$S_{13\%}$ paired cohort; (ii) S_S individuals clumped around L_S individuals, whereas the virtual $L_{34\%}$-$S_{13\%}$ spatial relationship was random. Large trees prevent landslide dislodgement of adjacent small trees through the nurse-plant effect. Our study suggests that landslide damage in sloping forests may be reduced simply by constantly maintaining a critical density of large trees.

Keywords: Facilitation, Forest Dynamics Plot, Nurse-plant Effect, Point Pattern Analysis, Slope Stability

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Introduction

Forests are known to reduce the impacts of shallow landslides through their abiotic mechanical and hydrologic properties (Johnson & Sitar 1990, Bovis & Jakob 1999, Walker & Shiels 2013). Shallow landslides in forests typically involve a sliding surface soil mass with a depth of up to 2 m (Stokes et al. 2009). The tensile and compressive resistance of tree roots increase the shear strength of shallow soils and, in turn, slope stability (Cohen & Schwarz 2017). Forests also reduce the pore water pressure of soils through rainfall interception and transpiration, thereby increasing the intrinsic mechanical strength of soil and the stability of a forested slope (Di Iorio et al. 2008, Schwarz et al. 2010).

Biotic interactions in forests are numerous and wide-ranging (Smith & Smith 2015), and can be negative (*e.g.*, competition – González De Andrés et al. 2018, Pretzsch 2022) or positive (*e.g.*, facilitation – Kothari et al. 2021, Pretzsch 2022), and interspecific (González De Andrés et al. 2018, Kothari et al. 2021) or intraspecific (González De Andrés et al. 2018, Pretzsch 2022). Biotic interactions between trees influence tree community properties, including trees' species diversity (LaManna et al. 2017), spatial distribution (Germany et al. 2019), and stem density (Magee et al. 2021). The likelihood of landslide occurrence has been related to tree species diversity (Genet et al. 2010, Osman & Barakbah 2011), spatial distribution (Roering et al. 2003, Cohen & Schwarz 2017, Cislaghi et al. 2021), and stem density (Fan & Lai 2014, Moos et al. 2016). It follows that tree-tree interactions should influence landslide occurrence through their effects on tree community properties. On the other hand, the intensity of plant-plant interactions varies with species diversity, individuals' spatial distribution, and stem density of plant communities (Smith & Smith 2015). Since landslides can substantially change these three properties of tree communities (Walker & Shiels 2013), landslides are likely to exert effects on tree-tree interactions through altering tree community properties. However, few studies explore the interplay between landslides and tree-tree interactions.

While biotic interactions between trees under post-landslide chronic stresses are

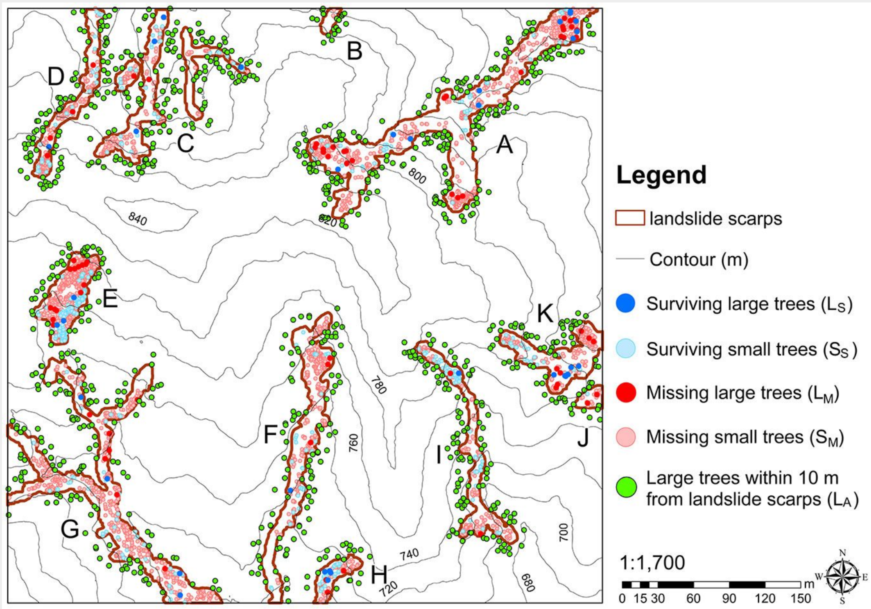

Fig. 1 - The spatial distribution of (a) the 11 landslides and (b) individuals of L_S, L_M, S_S, S_M and L_A. These landslides were caused by heavy rains of typhoons Kalmaegi and Sinlaku in 2008. L_S, L_M, S_S, S_M and L_A are the abbreviations for the cohorts of surviving large trees, missing large trees, surviving small trees, missing small trees, and large trees around the landslide scarps, respectively. Note that Landslides B and J were not included in our analyses due to their small area.

well appreciated (Walker & Shiels 2013), the processes by which the acute stresses of landslide dislodgement influence the post-landslide tree communities and tree-tree interactions are only beginning to be explored. Since landslides cause rapid plant mortality through uprooting and burial (Guariguata 1990), landslide dislodgement is a form of acute stress for plant survival. Although the loss of tree biomass is amongst the most noticeable landslide effects on forests, the processes by which landslides alter tree community structure are largely unknown because of the lack of pre-landslide vegetation data. Moreover, most previous studies disproportionally focused on how chronic stresses induced in landslide scarps, such as drought or high solar radiation, affect vegetation succession (Walker & Shiels 2013). Under acute landslide dislodgement stress, tree-tree interactions through roots, such as root grafting, may change tree survival rates. During dislodgement by landslides, the effects of proximate large trees on small tree survival will be negative if small trees in the root zones of dislodged large trees are likely to be removed or buried. Conversely, the biotic interactions between large and small trees will be positive if small trees in the root zones of surviving large trees are kept in place. Identifying the transition of tree community structure and tree-tree interactions associated with landslide dislodgement could provide new insights into landslide-prone forest management.

The present study aimed to identify landslide impacts on tree community structure and interactions between large and small trees under landslide dislodgement stress and to explore the role of such biotic interactions in slope stability. We asked: (i) does the diameter at breast height (DBH) distribution of trees surviving landslides differ from that of the pre-landslide tree communities; (ii) do landslides change the spatial relationships between large and small trees; (iii) is the role played by large trees negative or positive in the survival of small trees?

Materials and methods

Study area

The study site was located in the 25-ha Lienhuachih Forest Dynamics Plot (500 × 500 m), central Taiwan (23° 54′ 49″ N, 120° 52′ 43″ E). The elevation ranges from 667 m to 845 m a.s.l. (Fig. S1 in Supplementary material). This plot is characterised by steep terrain, with an average slope of 36° and a maximum of 77°. The annual precipitation is 2439 mm, with most falling in five months (May to September – Fig. S2). The mean annual temperature is 20.4 °C, with mean monthly temperatures ranging from 14.4 °C in January to 24.5 °C in July (Fig. S2 in Supplementary material).

The first tree census for this plot was completed in early 2008. Every tree with a diameter at breast height (1.3 m, DBH) equal to or greater than 1 cm was surveyed. The DBH, species identity, and location of 153,261 trees were recorded. This evergreen broad-leaved forest comprised 144 tree species from 46 families, dominated by Fagaceae, Lauraceae and Rubiaceae (Chang et al. 2012). The overall DBH distribution of tree species was negative exponential, indicating a high proportion of seedlings and saplings (Fig. S3 in Supplementary material). The maximum DBH was 115 cm, and trees with DBHs smaller than 20 cm accounted for 96% of the total stem number. The average overstorey canopy height measured by the airborne LiDAR was 11.4 m (Chung et al. 2019).

In 2008, typhoons Kalmaegi (maximum rainfall intensity, 450 mm/24 hr; date influencing Taiwan, 17-18 July) and Sinlaku (520.5 mm/24 hr; 14-15 September) caused 11 landslides in our study site (Chang et al. 2017). Most landslide scarps were relatively long and narrow, aligned along valleys (Fig. 1). Using the landslide classification system of Varnes (1978), the movement type was debris slide (LW Chang, unpublished data). The total disturbed area was 9159.47 m², and the areas of the largest and smallest landslides were 2561.62 m² (landslide A) and 83.85 m² (landslide B), respectively (Fig. 1). Landslides B and J were excluded from the following analyses due to their small areas (Fig. 1).

Data analysis

The depth of landslides was spatially heterogeneous in our study site (LW Chang, unpublished data). It is impossible to choose a threshold DBH with which we could precisely divide trees into large (the protectors against landslide dislodgement stress) and small trees (the protectees) because the threshold DBH should vary with landslide depth. Nevertheless, we selected 20 cm as the threshold DBH with the following approaches. If the threshold DBH is too low, many protectees will be misidentified as protectors. We rejected threshold DBHs of 30 cm and 40 cm, which yielded too few large trees to conduct statistically meaningful analyses. At 20 cm DBH, the 18 most dominant tree species in our study site reached the average overstorey canopy height of 11.4 m (GZM Song, unpublished data). Using the threshold DBH of 20 cm not only minimised the two analytical problems mentioned above but also has strong significance for its ecological (*e.g.*, light interception) and hydrological effects (*e.g.*, rainfall interception) of overstorey trees in our analyses.

The tree census conducted before the 2008 landslide event recorded 5,449 large trees (L cohort) and 147,812 small trees (S cohort) in the 25-ha plot. The pre-landslide population within landslide scarps created in 2008 was 3,643 trees, including 104 large trees (L_{PL} cohort, L for large tree and $_{PL}$ for pre-landslide) and 3,539 small trees (S_{PL} cohort, S for small tree – see Tab. S1 in Supplementary material). In addition, 934 trees (L_A cohort, $_A$ for around) were located less than 10 m away from the landscape scarps (Fig. 1, Tab. S1). Field surveys in 2009 showed that, after the 2008 landslide events, 35 large trees (L_S cohort, $_S$ for surviving) and 467 small trees (S_M cohort, $_M$ for missing) survived (Fig. S4, Tab. S1), which accounted for 34% and 13% of the pre-landslide populations, respectively (Chang et al. 2017). As a corollary, 66% of large trees and 87% of small trees were missing after the landslides.

To identify spatial relationships affected by biotic interactions between trees, four virtual tree cohorts were created through randomly selecting trees from the pre-landslide tree populations. The population sizes of the four virtual cohorts ($L_{34\%}$, $L_{66\%}$, $S_{13\%}$, and $S_{87\%}$) were identical to those of the L_S, L_M, S_S, and S_M cohorts, respectively. Using the $L_{34\%}$ cohort as an example, random selection was conducted through allocating a random number to each pre-landslide large tree (L_{PL}) and selecting those trees with numbers from the 1st to the 34th percentile ranks to create this virtual cohort, regardless of their location within the landslide area. The field-observed spatial patterns were removed from the virtual cohorts through random selection. As the population size of the virtual cohorts was controlled, inconsistent results of spatial analyses between the virtual and field-observed cohorts could only be attributed to their different spatial patterns, allowing us to identify trees' field-observed spatial patterns influenced by tree-tree interactions. In spatial analyses, large-tree cohorts were paired with small-tree cohorts in the same circumstances, *e.g.*, the cohort of missing large trees was paired with that of missing small trees (L_M-S_M paired cohort).

We located every small tree in the L_{PL}-S_{PL}, L_M-S_M, virtual $L_{66\%}$-$S_{87\%}$, L_S-S_S, and virtual $L_{34\%}$-$S_{13\%}$ paired cohorts first, and then the nearest large tree for each small tree with the computer program ArcGIS® v. 10.2 (ESRI, Redlands, California, USA). Ultimately, the distances from small trees to the nearest large trees for these paired cohorts were identified. Since the data of some tree cohorts were not normally distributed, differences between groups were always examined with the Mann-Whitney test (a nonparametric method) with Bonferroni correction (a method to counteract inflated Type I errors caused by multiple comparisons).

We used the O-ring statistic, one of the point-centred statistical methods, to explore the spatial relationships between large and small trees. The O-ring statistic is widely used in spatial distribution studies for organisms (Strimbu et al. 2017) and landslides (Zhang et al. 2010, Pourghasemi et al. 2020). The O-ring statistic includes univariate and bivariate analyses; the former estimates the spatial relationships of individuals in the same group, and the latter examines the spatial correlations between individuals of two groups (Pattern 1 and Pattern 2 – Wiegand & Moloney 2004, 2014). The present study used bivariate analyses, and large and small tree cohorts were treated as Pattern 1 and Pattern 2, respectively. The O_{12} estimate in bivariate analyses was calculated as the number of small tree individuals at a specific distance from the centre of the ring (a large tree) (Wiegand & Moloney 2004, 2014). The equation is (eqn. 1):

$$\hat{O}_{12}^{w}(r)=\frac{\sum_{i=1}^{n_i} Points_2\left[R_i^w(r)\right]}{\sum_{i=1}^{n_i} Area\left[R_i^w(r)\right]}$$

where $R_i^w(r)$ is the ring centred in the i^{th} large tree, with radius r and width w; $Points_2[R_i^w(r)]$ is the total point number of small trees in the ring $R_i^w(r)$; $Area[R_i^w(r)]$ is the area of the ring. If a value of O_{12} at a specific distance from a large tree is greater than the upper limit of the confidence belt, it indicates that small trees are clumped around large trees. Conversely, if the value of O_{12} is less than the lower limit of the confidence belt, it indicates a repulsion pattern between large and small trees. A value of O_{12} within the confidence belt represents a random spatial relationship between large and small trees. The O-ring analysis was conducted using the Programita software (Wiegand & Moloney 2014). The WM edge correction developed by Wiegand & Moloney (2004, 2014) was used to correct the edge effect.

The preliminary O-ring statistic showed that the clumped patterns of S_S trees were observed up to 13 m from L_S trees. Therefore, this distance was regarded as the maximum distance that the large-tree effects could reach in the survival rate analyses of small trees (SRSs). In the nine landslide scarps, the survival rate for small trees (SRSs) at selected distances (1-3 m, 3-5 m, 5-7 m, 7-9 m, 9-11 m, and 11-13 m) from L_S, L_M, and L_A individuals were analysed, namely SRS_{LS}, SRS_{LM}, and SRS_{LA}, respectively. Survival rates of small trees more than 13 m away from L_S, L_M, and L_A (SRS_N) were treated as small-tree survival in the absence of large-tree effects. The Mann-Whitney test (a nonparametric method) with Bonferroni correction was used to identify differences between these small-tree survival rates because of the non-normal distributions of small-tree survival rates.

Results

The DBH of surviving trees in the 2008 landslide scarps was significantly larger than that of missing trees and trees outside landslide scarps ($p < 0.01$, Mann-Whitney test with Bonferroni correction – Fig. 2). Moreover, tree survival rates increased monotonically with DBH (Fig. 3a), so the post-landslide communities had fewer smaller trees compared with the pre-landslide tree communities in the 25-ha plot and in the 2008 landslide scarps (Fig. 3b).

For the five paired cohorts (L_{PL}-S_{PL}, L_M-S_M, virtual $L_{66\%}$-$S_{87\%}$, L_S-S_S, and virtual $L_{34\%}$-$S_{13\%}$), the distances from small trees to the nearest large trees generally increased as their population size decreased (Fig. 4). The mean distance from S_{PL} individuals to the nearest L_{PL} individuals was 12.5 m. After the landslides, there were more missing trees (L_M, S_M) than surviving trees (L_S, S_S – Fig. 1), so that the distances from S_M individuals to the nearest L_M were lower than the distances from S_S individuals to the nearest L_S (Fig. 4). For the more numerous field-observed L_M-S_M and virtual $L_{66\%}$-$S_{87\%}$ paired cohorts, there was no significant difference between the two paired-cohorts ($p > 0.05$, Mann-Whitney test with Bonferroni correction). In contrast, for the less numerous field-observed L_S-S_S and virtual $L_{34\%}$-$S_{13\%}$ paired cohorts, the distances from S_S to the nearest L_S were lower than those from $S_{13\%}$ individuals to the nearest $L_{34\%}$ individuals ($p < 0.01$, Mann-Whitney test with Bonferroni correction – Fig. 4).

Among the six paired cohorts, the virtual $L_{34\%}$-$S_{13\%}$ paired cohort was the only one exhibiting a mostly random spatial pattern, while the other five showed clumped patterns (Fig. 5). Comparing the spatial patterns for those paired cohorts with identical population sizes, the L_M-S_M and the virtual $L_{66\%}$-$S_{87\%}$ paired cohorts were clumped (Fig. 5b, 5e), while the L_S-S_S and virtual $L_{34\%}$-$S_{13\%}$ paired cohorts exhibited different patterns (Fig. 5c, 5f). In contrast to the mostly random pattern of the virtual $L_{34\%}$-$S_{13\%}$ paired cohort, the clumped pattern of L_S-S_S paired cohorts indicated the mechanical

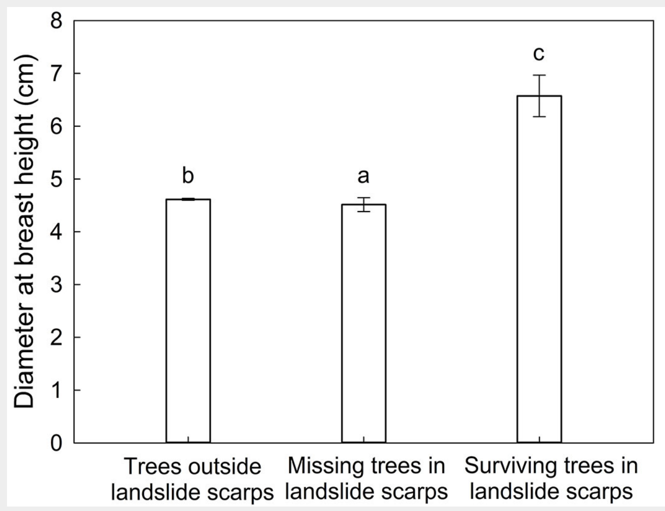

Fig. 2 - DBH of trees outside landslide scarps, missing and surviving trees in landslide scarps. Each bar and error bar respectively represent the mean and standard error of DBH in the same group. Different letters next to bars indicate significant differences ($p < 0.05$) between groups.

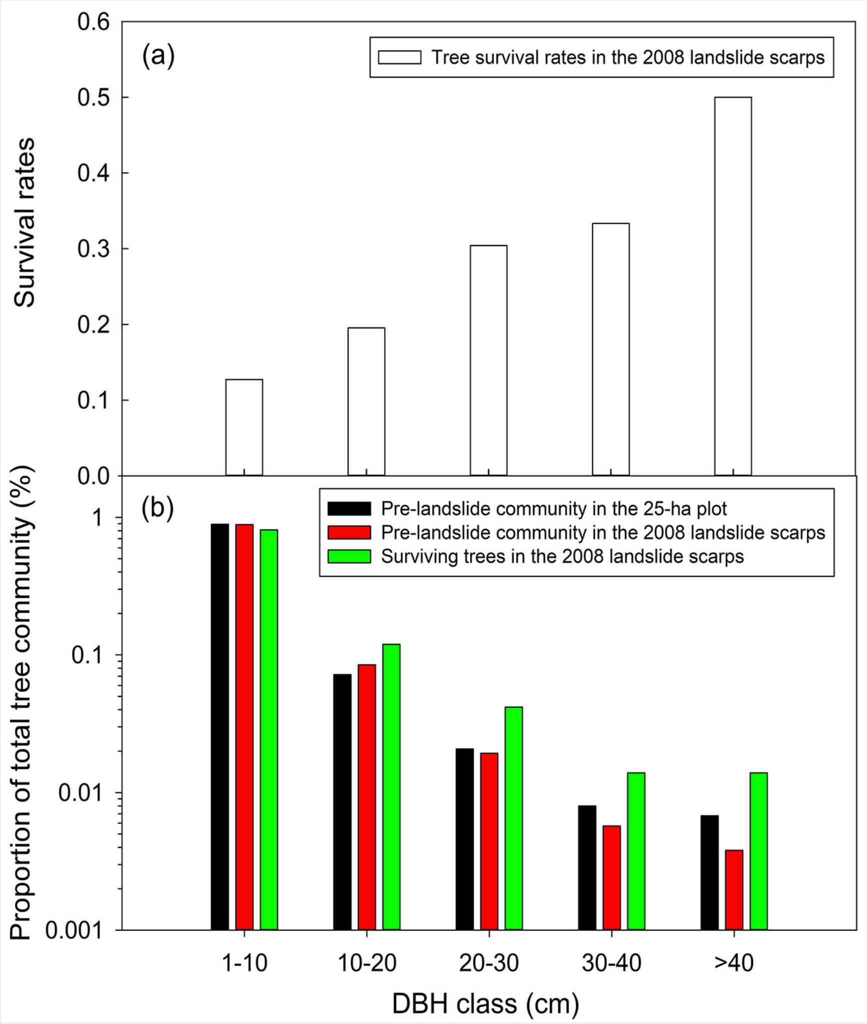

Fig. 3 - Landslide impacts on tree community structure. (a) Tree survival rates associated with DBH class in landslide scarps, and (b) the DBH distributions of the pre- and post-landslide tree communities. Each bar in panel (a) represents the overall tree survival rate of the nine landslide scarps for a DBH class.

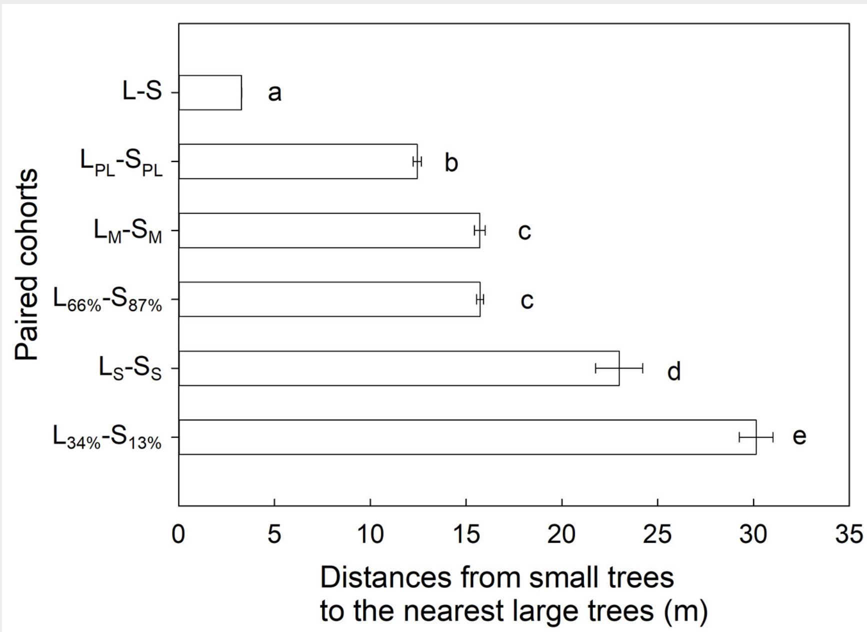

Fig. 4 - The distances from small trees to the nearest large trees for the five paired cohorts. Each bar and error bar respectively represent the mean and standard error of the distances from small trees to the nearest large trees in the nine landslide scarps. Different letters next to bars indicate significant differences ($p < 0.01$, Mann-Whitney test with Bonferroni correction) between groups. Please refer to the list of abbreviations for the definition of symbols.

supports of L_S individuals to S_S individuals under the dislodgement stress of landslides.

Although survival rates of small trees tended to increase with their distance from L_M individuals and decrease with their distance from L_S and L_A individuals, survival rates between groups did not differ significantly ($p > 0.05$, Mann-Whitney test with Bonferroni correction), except for those less than 3 m away from L_S and L_M trees (Fig. 6). SRS_{LA} and SRS_{LM} did not differ significantly from SRS_N (Fig. 6), indicating that the effects of L_A and L_M trees on the survival of small trees in landslide scarps were negligible.

Discussion

The role of large trees in the survival of small trees

The spatial patterns of the L_S-S_S paired cohorts were mainly determined by the nurse-plant effect, and the negative effects of large trees on small tree survival were trivial. In general, the distances from small trees to the nearest large trees increased as the tree population sizes decreased (Fig. 4). Although the population sizes of the field-observed L_S-S_S and virtual $L_{34\%}$-$S_{13\%}$ paired cohorts were identical, the dis-

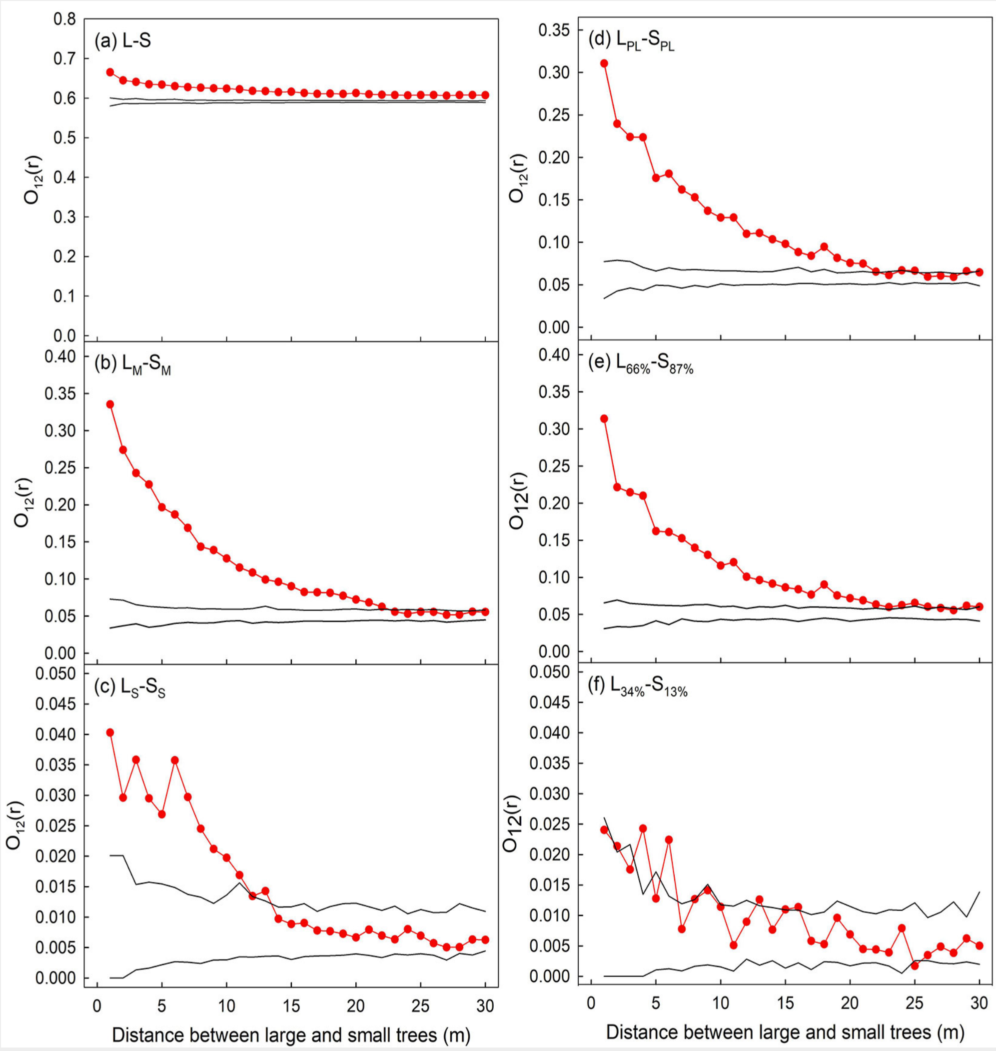

Fig. 5 - Spatial patterns of the five paired cohorts in Lienhuachih Forest Dynamics Plot: (a) L-S, (b) L_M-S_M, (c) L_S-S_S, (d) L_{PL}-S_{PL}, (e) virtual $L_{66\%}$-$S_{87\%}$, and (f) virtual $L_{34\%}$-$S_{13\%}$ paired cohorts. Two black curves represent the upper and lower borders of the 95% confidence belt. Red curves above and within confidence belts, respectively, indicate clumped and random distribution patterns between paired cohorts. Please refer to the list of abbreviations for the definition of symbols.

tances from S_S individuals to the nearest L_S individuals were significantly shorter than those from $S_{13\%}$ individuals to the nearest $L_{34\%}$ individuals. This phenomenon is attributed to the nurse-plant effect with which L_S saved small trees nearby from landslide dislodgment. On the other hand, the distances from S_M individuals to the nearest L_M individuals should be significantly shorter than those from $S_{87\%}$ individuals to the nearest $L_{66\%}$ individuals if small trees near L_M individuals tend to be dislodged. However, this was not the case (Fig. 4), indicating that the negative effect of missing large trees on small-tree survival was negligible.

The clumped spatial patterns of the L_M-S_M paired cohorts were mainly determined by the pre-landslide spatial patterns, and the effects of large trees on small tree survival were mainly positive. Post-landslide cohorts (L_M, L_S, S_M, and S_S) were sub-populations of the pre-landslide cohorts (L_{PL} and S_{PL}), so that the legacy of the pre-landslide spatial patterns should still be evident after the disturbance. The O-ring statistic showed that, prior to landslides, small trees clumped around large trees (Fig. 5a, Fig. 5d). Such a spatial pattern between small and large trees could result from in-

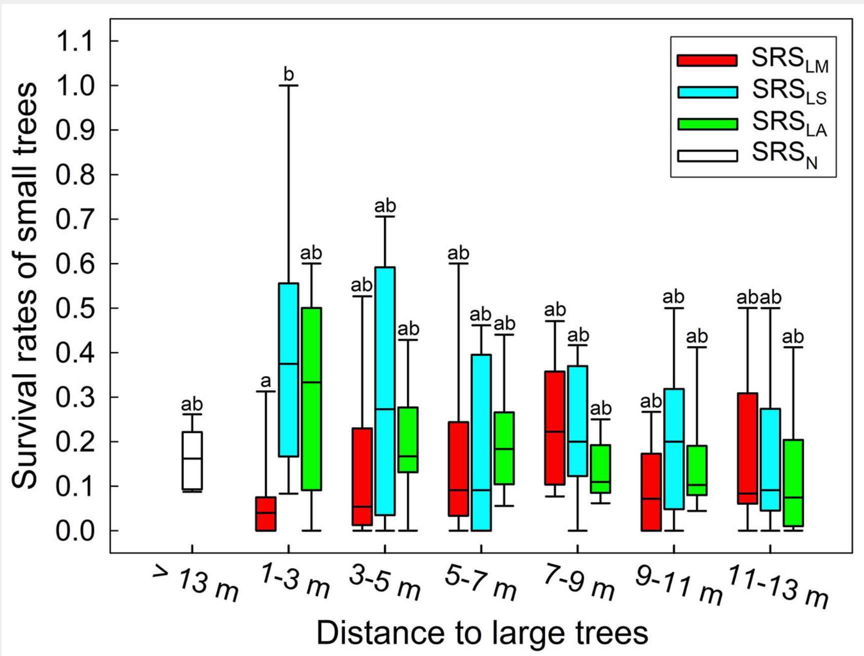

Fig. 6 - Survival rates of small trees (SRS_S) at different distances from L_M, L_S, and L_A individuals. SRS_N represents the survival rates of small trees without any large trees nearby. Different letters above boxes indicate significant differences ($p < 0.05$) between groups.

traspecific interactions (*e.g.*, the highest seed-fall density near the parent trees – Hubbell 1980), interspecific interactions (*e.g.*, beneficial mycorrhizal associations – Sasaki et al. 2019), or abiotic effects (*e.g.*, an uneven distribution pattern of the light environment – McClure & Lee 1993, favourable soil conditions). For the two virtual paired cohorts, the $L_{66\%}$-$S_{87\%}$ paired cohort exhibited a clumped spatial pattern similar to that of the paired L_{PL}-S_{PL} cohort, while the spatial pattern of the $L_{34\%}$-$S_{13\%}$ paired cohort was mostly random (Fig. 5d, Fig. 5e, Fig. 5f). These results showed a trend that the spatial correlation between the randomly selected large and small trees changed from clumped to random as the population size of the virtual cohorts decreased. In other words, random selection can remove the legacy of the pre-landslide spatial patterns if the population size of the virtual cohorts is reduced substantially. Therefore, the spatial pattern of the field-observed L_M-S_M paired cohort, which shared identical population size and similar spatial patterns with the virtual $L_{66\%}$-$S_{87\%}$ paired cohorts, should be attributed to the legacy effect (Fig. 5b, Fig. 5e). Since the virtual $L_{34\%}$-$S_{13\%}$ paired cohort exhibited a mostly random pattern, the clumped spatial pattern of the field-observed L_s-S_s paired cohort, which population size was identical to the $L_{34\%}$-$S_{13\%}$ paired cohort, should be attributed to a nurse-plant effect rather than reflecting the initial spatial pattern of the forest, or the legacy effect (Fig. 5c, Fig. 5f). In summary, under the dislodgement stress of landslides, the role of large trees in small tree survival was mainly positive.

Survival rate analyses also showed that large trees dislodged by landslides had negligible negative effects on small tree survival. Although the survival rates of small trees located 1-3 m away from L_M (SRS_{LM}) were significantly lower than those of small trees 1-3 m away from L_S (SRS_{LS}), the survival rates of small trees near L_M individuals (SRS_{LM}) were not significantly lower than that for small trees without large trees nearby (SRS_N – Fig. 6).

Mechanisms of the nurse-plant effect under landslide dislodgement stress

Large tree attributes associated with the survival of small trees after landslide dislodgement should vary with the inter-tree distance. Small trees within or at the edge of large-tree root zones, plus the soils in which they grow, are protected by direct mechanical support and anchorage of large-tree roots. Root grafting, which is the natural fusion of roots of different individuals (Lev-Yadun 2011), can increase the anchorage of trees in the root network and, in turn, raise their resistance to uprooting caused by winds, floods or landslides (Basnet et al. 1993, Lev-Yadun 2011). Although further studies are needed to identify the contribution of root grafting to the nurse-plant effect, crossing over of roots of different individuals is commonly observed in our root excavations for root pullout tests (GZM Song, personal observation), whereby large trees can provide direct mechanical support to small trees.

The protection zones for small trees of L_S individuals could be as wide as 13 m (Fig. 5c), which was much greater than the field-observed radii of tree root zones in our study site (GZM Song, personal observation). Within single landslides, S_S individuals were significantly closer to the landslide heads than L_S individuals ($p < 0.01$, Mann-Whitney test – Fig. S5 in Supplementary material), suggesting that buttressing and arching of L_S roots may have protected small trees even beyond the limits of their root zones. Due to the slope toe protection provided by trees, a location directly upslope from a large tree may be stabilised even though its roots do not reach that point (Cohen & Schwarz 2017). This is the so-called buttressing effect. If the distances between trees at hillslope toes are short enough, soil masses with no tree directly down the slope are still stabilised by the root arching effect (Fan & Lai 2014). Similarly, forests on the path of debris flow reduce debris-flow runout and, in turn, protect downslope trees or infrastructure (Bettella et al. 2018). Since most landslides in our study site occurred in valleys or close to drainage lines (Fig. 1), surviving large trees may have intercepted debris flow and, in turn, reduced the extent of mechanical damage to small trees. Further studies are needed to verify the roles of these effects in the tree-tree interactions under the dislodgement stress of landslides.

Landslide impacts on tree community structure

Landslides change tree community structure by removing more trees of smaller DBHs. Post-landslide tree survival is a result of the interplay between landslide depth and root depth. Tree roots must reach soils deeper than those displaced by landslides if they are to survive landslides. The mean depth of landslides in our study site was 1.25 m (LW Chang, unpublished data), which would allow deeper-rooted trees to survive. Root depth tends to increase with the DBH of trees (Genet et al. 2008). Therefore, in the present case, the DBHs of surviving trees were higher than those of missing trees (Fig. 2), and tree survival rates increased with their DBHs (Fig. 3a). Although landslides lowered the proportion of stem number in small DBH classes, the post-landslide tree community structure maintained a negative exponential DBH distribution (Fig. 3b). Such a community structure was partly a result of the nurse-plant effect with which surviving large trees reduced small tree mortality caused by landslides. The negative exponential DBH distribution is an indication of sustainable tree populations and communities (Rubin et al. 2006). In addition, these landslide scarps were surrounded by forests, so tree recruitment could be promoted by seed rains from neighbouring trees. It is expected that the tree community structure in landslide scarps in the study area will remain negative exponential in the future.

Suggestions for landslide-prone forest management and future studies

The nurse-plant effect of large trees should be incorporated into the management of landslide-prone forests. Due to the facts that root reinforcement is mainly contributed by large roots (Giadrossich et al. 2019) and larger trees develop more large roots than do small trees, large trees survived landslides better than did small trees (Fig. 2, Fig. 3). Surviving large trees protected small trees from landslide dislodgement (Fig. 4, Fig. 5) so that soils occupied by these small trees were kept in place. Although root reinforcement from the remaining roots of logged trees will not vanish until a few years later, root decomposition following clearcutting practices may increase landslide risks for several years (Bischetti et al. 2016, Vergani et al. 2016). Silvicultural practices associated with retaining large trees, such as the systems of single tree selection, seed tree, or shelterwood (Pommerening & Grabarnik 2019), are recommended to reduce soil loss due to landslides. Results of the present study (Fig. 6), Cislaghi et al. (2021) and Moos et al. (2016) indicated that, to maximise the protective effects of large trees, their spacing distance should be kept below 6 m (*i.e.*, average stem density ≥ 256 stem ha^{-1}).

In addition to the acute dislodgement stress of landslides, large trees surviving landslides can ease the chronic post-landslide stresses and, in turn, shorten the time of vegetation recovery. Post-landslide habitat degradation poses several chronic stresses for plant colonisation, such as excessive solar radiation and soil erosion associated with vegetation removal and soil nutrients loss due to topsoil removal (Wilcke et al. 2003, Lin et al. 2006, Walker & Shiels 2013, Chang et al. 2017). The long-term colonisation of persistent pioneer plants can further retard the establishment of late-successional species and, in turn, arrest vegetation succession (Guariguata 1990, Myster & Sarmiento 1998, Royo & Carson 2006). Through intercepting strong sunlight, providing materials for soil organic matter enrichment, and suppressing the growth of persistent pioneer plants, large trees in or near landslide scarps can exert positive effects on the growth and survival of recruited and existing small trees and ultimately promote vegetation recovery (Walker & Shiels 2013, Chen et al. 2014).

Improved management of forests susceptible to landslides requires more studies to unveil the interplay between tree-tree biotic interactions and landslides. Our results showed that the nurse plant effect reduces small tree mortality in landslides. Therefore, increasing or at least maintaining a critical stem density of large trees can be employed as both preventative (reducing tree loss to landslides) and restorative strategies (easing post-landslide drought and harsh sunlight effects) for hillslope forest management. On the other hand, broader biotic interactions may also influence landslide phenomena. For example, allelopathy, mycorrhizal systems, and the Janzen-Connell effect may change tree community properties (*e.g.*, root density, spatial distribution, stem density – Germany et al. 2019, Sasaki et al. 2019, Hierro & Callaway 2021) and, in turn, the likelihood and impact of landslide occurrence. Further detailed studies linking biotic interactions to landslide occurrence would enable biotic interactions to be incorporated into management tools for landslide-prone forests.

Conclusion

The present study aimed to examine how shallow landslides influenced the structure and tree-tree interactions of tree communities. Although landslide survival increased with increased tree DBH, the DBH distribution of the post-landslide tree community structure retained the negative exponential form of the pre-landslide forest. Landslide impacts on tree regeneration were expected to be trivial due to this continuity of community structure and the numerous trees surrounding landslide scarps. The nurse-plant effect of large trees on small tree survival in landslide scarps was identified by two phenomena: the clumping of surviving small trees around surviving large trees, and the significantly smaller mean distance between members of surviving large and small tree paired cohorts compared with the corresponding virtual paired cohort. The survival rates of small trees within 3-13 m from missing large trees were not significantly lower than those with no large trees nearby, indicating that large trees did not increase the mortality of adjacent small trees once they were dislodged. Our study established that interactions between large and small trees under the dislodgement stress of landslides were mainly positive and that such biotic interactions can reduce tree mortality resulting from landslides. We suggest that hillslope forests susceptible to shallow landslides should be managed through the simple procedure of maintaining a specified minimum density of large trees and recommend further studies into the relationships between biotic interactions and landslides.

List of abbreviations

(L): the cohort of large trees recorded in the 25-ha plot before the 2008 landslide event; ($L_{34\%}$, $L_{66\%}$): cohorts consist of trees randomly drawn from L_{PL}. The percentage indicates their population size related to that of the L_{PL} cohort; (L_S): the cohort of surviving large trees in the 2008 landslide scarps; (L_M): the cohort of large trees removed by the 2008 landslides; (L_A): the cohort of large trees less than 10 m away from the 2008 landslide scarps; (L_{PL}): the cohort of pre-landslide large trees in the 2008 landslide scarps; (S): the cohort of small trees recorded in the 25-ha plot before the 2008 landslide event; ($S_{13\%}$, $S_{87\%}$): cohorts consist of trees randomly drawn from S_{PL}. The percentage indicates their population size related to that of the S_{PL} cohort; (S_S): the cohort of surviving small trees in the landslide scarps; (S_M): the cohort of small trees removed by the 2008 landslides; (S_{PL}): the cohort of pre-landslide small trees in the 2008 landslide scarps; (SRS_N): survival rates of small trees which were at least 13 m away from L_S, L_M, and L_A; (SRS_{LS}): survival rates of small trees near L_S; (SRS_{LM}): survival rates of small trees near L_M; (SRS_{LA}): survival rates of small trees near L_A.

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Authors Contribution

Jian-Hong Yang: Conceptualisation, Data Curation, Formal analysis, Methodology, Visualisation, Writing - Original Draft, Writing - Review & Editing. Li-Wan Chang: Data Curation, Funding acquisition, Investigation. Kai-Chi Hsu: Project administration, Writing - Review & Editing. Chia-Cheng Fan: Validation, Writing - Review & Editing. David Doley: Writing - Review & Editing. Guo-Zhang M. Song: Conceptualisation, Funding acquisition, Methodology, Project administration, Supervision, Visualisation, Writing - Original Draft, Writing - Review & Editing.

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Supplementary Material

Fig. S1 - Location of Lienhuachih Forest Dynamics Plot.

Fig. S2 - Climate diagram of Lienhuachih Forest Dynamics Plot.

Fig. S3 - DBH class distribution of the pre-landslide tree community in the 25-ha Lienhuachih Forest Dynamics Plot.

Fig. S4 - DBH class distribution of surviving and missing trees in landslide scarps and large trees within 10 m away from landslide scarps.

Fig. S5 - Elevation differences between landslide heads and surviving trees, L_S and S_S.

Tab. S1 - Species, stem number and basal area of surviving large trees (L_S), missing large trees (L_M), surviving small trees (S_S), missing small trees (S_M) in landslide scarps and large trees within 10 m from landslide scarps (L_A) in Lienhuachih dynamics forest plot.

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