

Biochar-Based Seed Coating as an Effective Strategy to Reduce Seed Predation When Restoring Forests on Degraded Land

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Abstract

As ecosystem degradation becomes more widespread, there is a growing need for efficient and effective forest restoration methods. Direct seeding is one such method that can be used to cover a relatively large area, particularly places with difficult-to-access terrain. One major obstacle hampering successful restoration via direct seeding is seed predation, as seeds are damaged or eaten. We tested the effectiveness of encrusting six species of native seeds with biochar-based coating in reducing the seeds' chances of being predated on degraded hillsides and landslide scars in Hong Kong. The six seeded species are native trees and shrubs, including both late-successional and pioneer species that are present in forests and shrublands. Our results show that biochar-based seed coats were able to significantly reduce overall seed predation by 5.77% (SE = 1.41, $p < 0.05$). Additionally, we found varied effectiveness of the biochar-based seed coats across species and seed morphology. Of the six species that were included, four of them had significantly reduced seed predation after encrusting with biochar-based seed coats, while two other species were not significantly affected by the biochar-based seed coats. When we investigated seed predation against seed morphology, we found that while the species with larger seeds were more likely to be predated when sown without any biochar-based seed coat, the effectiveness of the biochar-based seed coat to reduce predation also increased with larger seeds. Our results suggest that encrusting seeds with biochar-based seed coats is an effective means of reducing seed predation.

Keywords

Biochar, Forest Restoration, Hong Kong, Seed Coating, Seed Predation

1. Introduction

As widespread environmental degradation caused by humans continues, the United Nations has proclaimed the United Nations Decade on Ecosystem Restoration 2021-2030. It aims to prevent, halt, and reverse the degradation of ecosystems for the benefit of people and nature. To achieve this goal, various ecological restoration techniques have been used to assist in the recovery of degraded ecosystems (Wortley et al., 2013), restoring lost biodiversity, and increasing the provision of ecosystem services (Benayas et al., 2009). Ecosystem restoration is particularly pertinent in urban areas where some of the most intensive developments, and thus ecosystem degradation, have occurred (Miller & Hobbs, 2002) and where intense landscape fragmentation has led to high barriers to natural seed dispersal (Overdyck et al., 2013; Wallace & Clarkson, 2019).

Conventionally, forest restoration through the planting of seedlings can speed up the recovery of degraded hillsides (Holl et al., 2011). Upon successful development of seedlings, a new canopy cover is formed, which helps improve soil properties and micro-climate on degraded lands (Chen et al., 2014). Planting seedlings in patches and tree islands on degraded forests can also promote bird visitations and seed dispersal (Fink et al., 2009). Eventually, forest recovery on degraded hillsides can be enhanced through plant establishment and vegetation succession (Holl, 2002). Despite promising results from previous studies, forest restoration by conventional tree planting is not feasible on landslides due to the steepness and inaccessibility of slopes (Pang et al., 2018). Owing to the frequent occurrence of landslides under high seasonal rainfalls, intense soil erosions further deteriorate soil conditions and hinder vegetation growth (Chen et al., 2014; Lee et al., 2020). Without a stable layer of topsoil, it is difficult to retain nutrients and mycorrhizal inoculum on landslide trails (Adams & Sidle, 1987; Dalling & Tanner, 1995). Under these harsh conditions, vegetation succession is often limited, leading to forest restoration failure (Siddique et al., 2008). To overcome these barriers, alternative restoration strategies are needed to successfully establish plants on landslide scars.

Direct seeding is one such method that can help boost forest recovery after degradation (Lamb et al., 2005; Dimson & Gillespie, 2020). Previous studies have shown that direct seeding can increase seed availability of late-successional species, allowing them to establish on degraded forests where seed dispersal was limited in the past (Cole et al., 2011). Direct seeding of pioneer species can suppress the growth of invasive grasses and weeds by shading out light under their canopy cover (Lamb et al., 2005), while sowing both pioneer and late-successional species on degraded hillsides has been shown to have high germination rates and can lead to earlier establishment of a mature forest (Law et al., 2023; Martínez-Garza et al., 2005).

However, the effectiveness of landslide restoration by direct seeding is still limited, and seed predation is a major obstacle to seed survival, and thus restoration success when implementing direct seeding to restore degraded landscapes (Pearson et al., 2019; Taylor et al., 2020). Rodent granivores can be particularly detrimental

to restoration efforts using direct seeding as they can suppress seed recruitment, establishment, and growth of individual plant species (Hau, 1997; Maron et al., 2012). Similarly, insects have been shown to play a prominent role in affecting restoration dynamics (Linabury et al., 2019). Previous studies have shown that seed traits, such as seed size and seed mass, have varying effects on the foraging preference of granivores (Gong et al., 2015; Moles et al., 2003). The smaller seeds of pioneer species can be prone to seed predation (Garcia-Orth & Martínez-Ramos, 2008). For these seeds, fire ants, cutter ants, and harvester ants are major seed predators, often carrying the small seeds back to their underground nests (Nepstad et al., 1996). Small seeds are also vulnerable to rodents after direct seeding, removing local seed banks rapidly (Anderson & MacMahon, 2001; Busch et al., 2012). Similarly, large-seeded species such as Fagaceae also suffer serious seed predation by rodents in degraded hillsides (Hau, 1997). As a result, techniques that prevent seed predation or removal are important in helping increase seed establishment and restoration success where seed predation pressure is high.

Seed coating can be a potential method to help reduce seed predation (Taylor et al., 2020). Seed coating is the process of covering natural seeds with additional materials and is done for a variety of reasons, including modifying the physical properties of the seeds (Pedrini et al., 2017), to provide a nutritive and water-holding medium for root development (Brown et al., 2019), or to introduce a deterrent to seed predation (Pearson et al., 2019). Commonly used in the agricultural sector, the use of seed coating as a means to restore degraded landscapes has also increased in popularity in recent years (Madsen et al., 2016). Concurrently, biochar has also been gaining popularity as a soil enhancer to help improve soil quality in heavily degraded regions (Ding et al., 2016). Biochar is produced through the process of pyrolysis, the heating of organic materials in an oxygen depleted atmosphere, and has been shown to lead to a strong positive tree growth response when used for forest restoration (Thomas & Gale, 2015). Biochar has also been shown to be able to enhance seed germination (Thomas, 2021; Law et al., 2023), improve soil water retention (Razzaghi et al., 2020), and reduce nutrient leaching loss (Biederman & Harpole, 2013). Several mechanisms have been proposed to explain how seed coating can deter seed predation by granivores (Taylor et al., 2020). Biochar-based seed coating could mask the scent of seeds, reducing their attractiveness to seed predation by potential granivores. Biochar-based seed coating may also be unpalatable to animals (Pearson et al., 2019; Taylor et al., 2020). Alternatively, biochar-based seed coating may reduce seed predation by changing the physical morphology of the seeds. The addition of a seed coat can increase the handling time of the seeds by adding a physical barrier between the granivore and the seed (Jacobs, 1992; Taylor et al., 2020), increasing the time cost needed for the animals to consume the seeds. Moreover, granivores may avoid eating biochar-based encrusted seeds due to neophobia (novel food avoidance) (Taylor et al., 2020).

Biochar's potential to reduce seed predation, particularly in Hong Kong's

degraded lands, remains untested. As a city, Hong Kong has undergone substantial forest restoration, via both natural regeneration and active restoration, after being heavily deforested in the middle of the 20th Century (Dudgeon & Corlett, 1994). While intensive reforestation has taken place in the city in more recent years (Corlett, 1999), there are still plenty of opportunities for further reforestation across the city's landscapes. This is particularly important for degraded hillsides and landslide scars, which are very prevalent across the city (Wang et al., 2021), as more than 60% of land here has slopes of over 15°, and thus many slopes are susceptible to landslide events under high seasonal rainfalls (Choi & Cheung, 2013). Ecologically, landslides are one of the main threats to the city's existing forests (Wang et al., 2021; Law et al., 2023). Landslides can cause significant ecological damage, wiping out forests, destroying habitats, and removing the topsoil and viable seeds from the slope (Guariguata, 1990; Geertsema et al., 2009). The remaining soil is usually severely degraded and nutrient-poor, limiting the natural regeneration of the landslide scars (Aide & Cavelier, 1994), leading to higher risks of repeated landslides (Pang et al., 2018). Hong Kong's natural forests also often have arrested succession due to frequent typhoons (Abbas et al., 2020) and a lack of large mammalian frugivores (Dudgeon & Corlett, 2004), affecting the establishment of mature forests. Active restoration through direct seeding is one way to encourage the vegetation recovery of landslide sites (Law et al., 2023), reducing future risk of repeated landslides by reducing soil erosion (Lin et al., 2006), especially in tropical and subtropical regions (Wang et al., 2020).

Using plots in Hong Kong as a case study, we aimed to investigate the potential effectiveness of using biochar-based seed coat to reduce seed predation in the field, where rodents, wild boars (*Sus scrofa*), birds, and insects are all potential seed predators that can hinder forest recovery projects that make use of direct seeding (Hau, 1997; Chung & Corlett, 2006). We addressed three specific questions in this study: 1) Does treating seeds with biochar-based seed coating reduce seed predation? 2) Does the seed coat treatment have different effectiveness for seeds from different species? 3) What seed traits determine the effectiveness of the seed coat treatment?

2. Methods

2.1. Study Sites

The study was conducted across six sites in Hong Kong (22°23'47.0"N, 114°06'34.2"E) in 2021 and 2022. The pilot experiment was conducted across three degraded hillsides in the New Territories of Hong Kong, where most of the areas are eroded and support only sparse vegetation, exposing the soil with very little canopy cover (Table S1). These were located at Tsing Yi (22°20'45.1"N, 114°05'39.1"E), Sham Tseng (22°22'03.6"N, 114°03'08.3"E), and Ha Fa Shan (22°22'41.9"N, 114°05'57.3"E) (Figure 1). Minimal human disturbances, such as burning and cutting, were observed at all sites except for occasional hikers passing by the Tsing Yi site.

The main experiment was conducted at three sites, which were landslide trails

formed on 29th August 2018 after a severe rainstorm. These were located at Kam Tin (22°26'11.8"N, 114°06'14.8"E), Ta Shek Wu (22°27'50.5"N, 114°06'13.9"E), and Sandy Ridge (22°31'41.2"N, 114°07'09.7"E), all within the New Territories of Hong Kong (Figure 1). In Kam Tin and Ta Shek Wu, no recent signs of human disturbance were observed, while frequent hill fires were recorded at the Sandy Ridge site (Table S2). Landslides were recorded in these three sites within three years prior to the experiment.



Figure 1. Locations of the study sites across the New Territories, Hong Kong.

2.2. Seed Collection and Preparation

The pilot experiment included three native Hong Kong species: *Lithocarpus corneus*, *Polyspora axillaris* and *Cyclobalanopsis myrsinifolia*. The main experiment included three additional native Hong Kong species: *Reevesia thyrsoidea*, *Ormosia semicastrata* and *Elaeocarpus sylvestris*. All seeds were collected during the winter fruiting season between September and March in Hong Kong from at least three mother trees per species. These species were chosen based on different successional stages, seed sizes, dispersal mode, and seed availability (Table S3). Additionally, *L. corneus* has additional conservation value, as most colonies are restricted to isolated upland areas and montane forests in Hong Kong, where they are threatened by seed predation and the lack of seed dispersal agents (Chan, 2001; So, 2004; Strijk, 2018).

After seed collection, the cupule and membranous wings of seeds were removed. For storage, the seeds of *L. corneus* and *C. myrsinifolia*, which are recalcitrant, were placed in aluminium foil containers with moistened sand to maintain stable seed moisture content and minimise unwanted physiological changes in seeds. These seeds were then stored in a refrigerator at 5°C to 10°C, which simulated cold stratification and helped break dormancy (Baskin et al., 2006). Small

seeds like *E. sylvestris*, *O. semicastrata*, *P. axillaris* and *R. thyrsoides*, on the other hand, can resist desiccation, and hence, they were directly stored in zip-top bags at room temperature. These plastic bags were unzipped to avoid excessive moisture and prevent moulding.

2.3. Preparation of Biochar-Based Encrusted Seeds

Biochar-based encrusted seeds were prepared five days before the commencement of the experiment. The biochar is composed of mixed woods, mainly *Acacia confusa*, *Dimocarpus longan* and Bauhinia species. The woody debris was heated in closed chambers at around 500°C under low oxygen for half an hour (James & Aronson, 2017). Subsequently, fine powders of biochar (active ingredient) and clay (filler) were ground up and the biochar powders were mixed with clay powders at a 6:4 ratio. After thorough mixing, water was added until the powder mixture reached optimum moisture with binding properties. The smaller seeds of *P. axillaris*, *R. thyrsoides* and *O. semicastrata* were wrapped in the powder mixture, and then rolled by hand to produce biochar-based encrusted seeds. The larger seeds of *L. corneus*, *C. myrsinifolia* and *E. sylvestris* were produced using a sweet rice ball forming machine (Model YX-65, China; Figure S1). These seeds were first moistened, then rolled with a dry powder mixture to produce biochar-based encrusted seeds. All encrusted seeds were produced with a coating of 0.5 cm (around 10 g and 20 g of powder mixture for smaller and larger seeds respectively), and dried at room temperature to achieve a hard coating surface.

2.4. Experimental Design

In the pilot experiment, in each of the three degraded hillside sites, a 20 m transect was established. Along each transect, five plastic seed trays (21.5 cm × 26 cm × 4 cm) were evenly spaced at intervals of 5 m. Each seed tray was divided into equally sized subunits (4.3 cm × 4.3 cm), and all subunits were physically separated. Each column consisted of six subunits and within each subunit, one seed for each treatment (biochar-based encrusted seeds or raw seeds) of *L. corneus*, *P. axillaris*, and *C. myrsinifolia* were sown in random order. Each column was then repeated five times per tray (Figure 2). A total of 450 seeds within 15 trays, each including 15 biochar-based encrusted seeds and 15 raw seeds, were sown at each degraded hillside site.

In the main experiment, in each of the three landslide sites, five plastic seed trays (21.5 cm × 52 cm × 4 cm) were randomly distributed along the landslide trail. A transect wasn't used as they were impossible to establish on the landslide trails. Within these sites, each seed tray was divided into equally sized subunits (4.3 cm × 4.3 cm), and all subunits were physically separated (Figure 2). Each column consisted of twelve subunits and within each subunit, one seed for each treatment (biochar-based encrusted seeds or raw seeds) of the six experimental species was sown in random order. Each column was then repeated ten times per tray (Figure 2). A total of 1800 seeds within 15 trays, each including 60 biochar-

based encrusted seeds and 60 raw seeds, were sown at each landslide site. All seed trays from all sites were buried 3 cm underground to fix them in place. A thin layer of soil (~3 cm) was filled in each seed tray, which simulated the natural environments from each site.

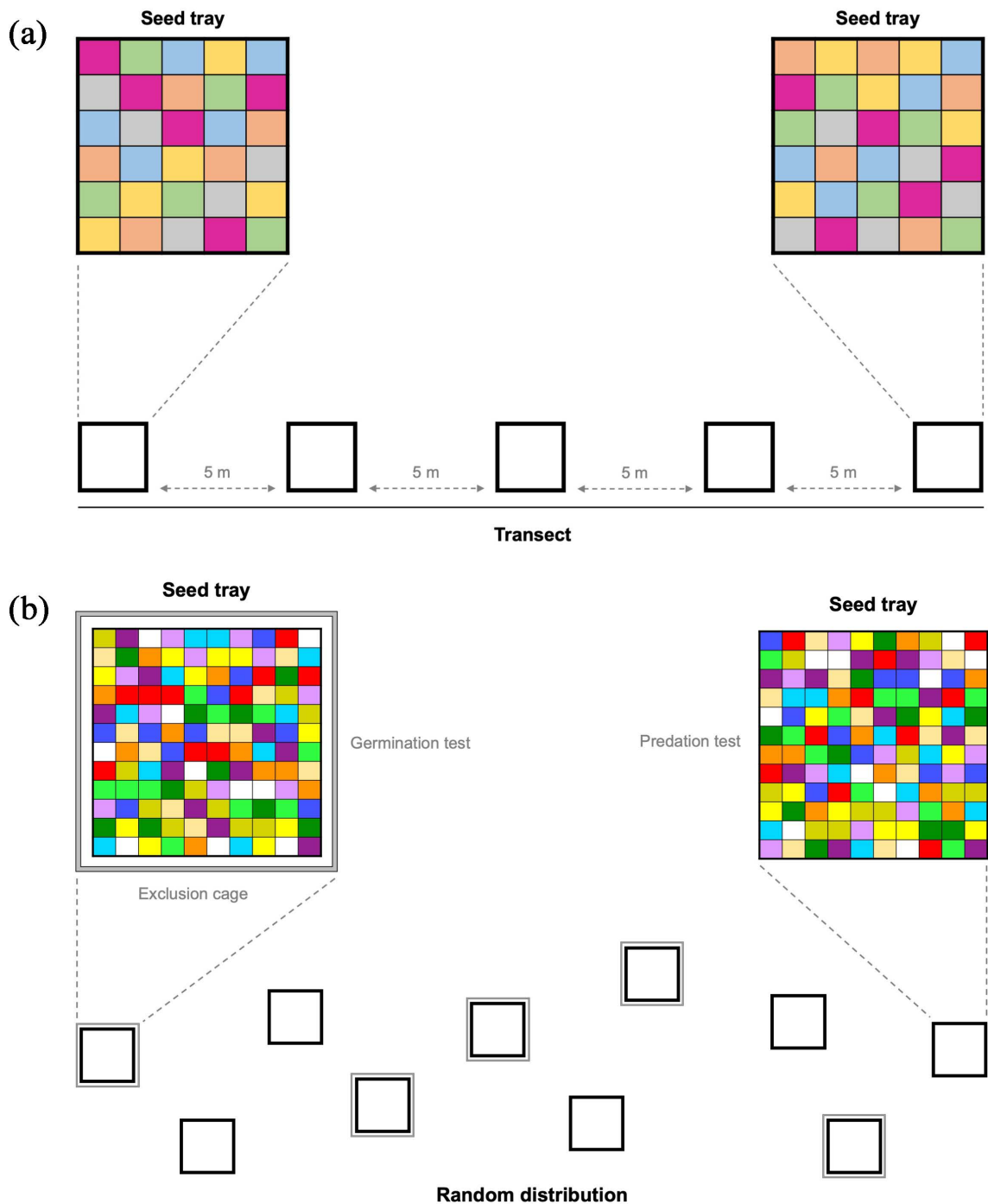


Figure 2. Example illustration of seed tray arrangement across (a) the three hill side sites and (b) the three landslide sites. Each small square represents a subunit (4.3 cm × 4.3 cm). Each colour represents one combination of species and treatment, which were randomly distributed along each column. The columns were then repeated (a) 5 times or (b) 10 times.

To investigate the potential effects seed traits might have on seed predation, we also estimated average seed traits, including seed size, seed dry mass, seed thickness, seed width, and seed density, by randomly selecting ten seeds and calculating the mean for each seed trait.

2.5. Monitoring

Each of the seed trays was censused 16 days after the trays were placed. During each census, seeds were classified into three categories: present, lost, or damaged and the number of seeds in each category was counted. Intact seeds were counted as “present”, while missing seeds were counted as “lost”. Seeds were defined as “damaged” under the following conditions: 1) toothmark(s) present on the surface of seeds; 2) seeds were partially eaten or peeled; 3) fragments of seeds were left on trays.

2.6. Statistical Analysis

Due to the differences in study designs and species included, the data from the pilot and main experiments were analysed separately. For both experiments, we used mixed-effect logistic regressions to analyse the data. These were conducted using R (version 4.2.1; R Core Team, 2022) and the lme4 package (Bates et al., 2015). For both experiments, we used the proportion of seeds predated (either lost or damaged) as the response variable. Additionally, all models included tray number nested within the study site as a random effect. To investigate the effectiveness of biochar-based encrusted seeds overall and across the different species, we used species and treatment as our explanatory variables. To further investigate potential differences in the effectiveness of the biochar-based seed coats, we fit additional models using treatments and each of the seed traits (seed size, seed dry mass, seed thickness, seed width, and seed density) individually as explanatory variables. Each of these was scaled and centred before being used as variables in the models. Each model included only one seed trait, as these were all highly correlated with each other. The seed trait variables were standardised to ensure model convergence.

Additional models, including data from both experiments, were also constructed, as while their experimental designs differed, we can assume the data to have roughly equal variances. These models used the larger sample sizes of the combined dataset, but also included an additional parameter, “experiment”. We investigated a three-way interaction between species, treatment, and experiment in this model, along with the tray number nested within the study site, as a random effect that was identical to the separate models. We tested whether the three-way interaction improves the model, comparing it against models with only two-way interactions and the null model.

3. Results

Across both pilot and main experiments, we found that applying biochar-based

seed coats to the seeds significantly decreased the overall percentage of seeds that were predated (pilot experiment: 3.92%, SE = 1.30, $p = 1.49e-7$; main experiment: 6.20%, SE = 1.28, $p = 1.51e-13$). However, we also found that the effects of the seed coat treatments varied across the different species tested, with significant interactions between species and treatment. **Figure 3** shows that when focusing on the main experiment and only on the raw seeds, *L. corneus* had the highest proportions of seeds predated, followed by *C. myrsinifolia*, *P. axillaris*, and *R. thyrsoidea*. Even when planted as raw seeds, *E. sylvestri* and *O. semicastrata* had relatively low proportions of seeds predated.

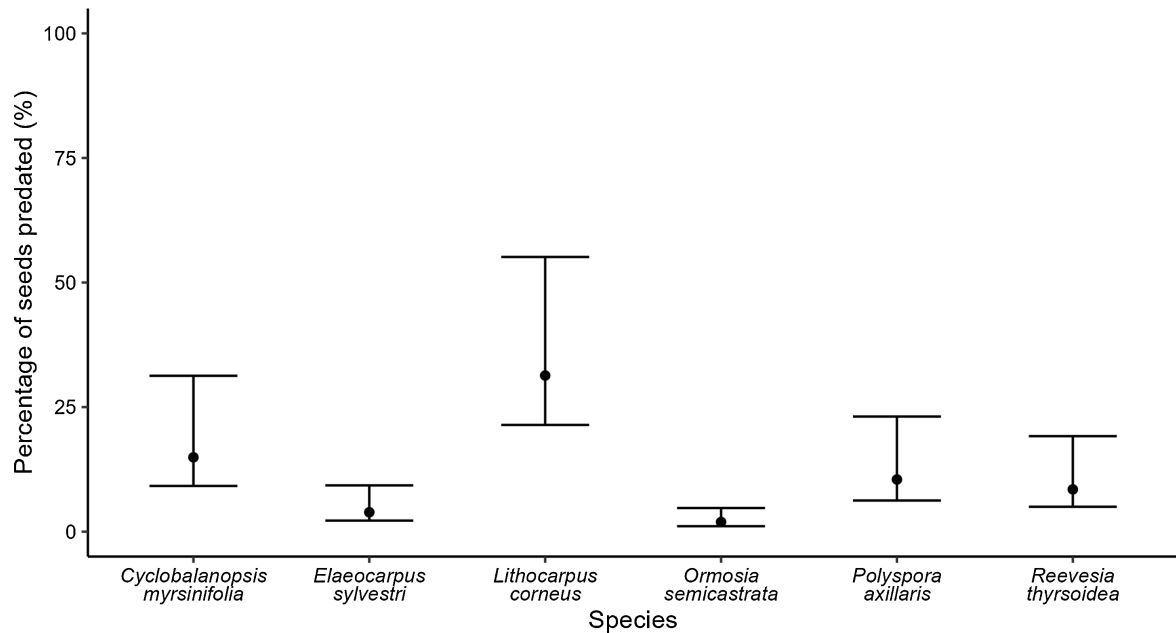


Figure 3. Differences in the percentage of seeds predated when sown without any treatment within seed trays of six different species. Error bars denote 95% confidence intervals.

Investigating the differential effects of biochar-based encrusted seeds, we found that for four of the six species (*E. sylvestri*, *L. corneus*, *P. axillaris*, and *R. thyrsoidea*), the biochar-based encrusted seeds had significantly fewer seeds predated than the raw seeds (**Figure 4**). For *C. myrsinifolia*, the seed coat treatment reduced predation on the seeds, but the difference was not significant. For *O. semicastrata*, as the raw seeds had very few seeds predated, the seed coat treatment had minimal effect on seed predation. Moreover, there were also substantial differences in seed predation between sites observed for some species, as shown by the relatively larger confidence intervals shown in **Figure 4** for raw seeds.

Further investigating the relationship between seed predation and seed traits, we found that all the seed traits we tested (dry mass, thickness, size, and density) significantly affected the proportion of seeds that were predated. Specifically, **Figure 5** shows that increases in seed dry mass, thickness, size, and density all led to significant increases in the proportion of seeds that were predated.

Looking at the effects of seed traits on the effectiveness of biochar-based

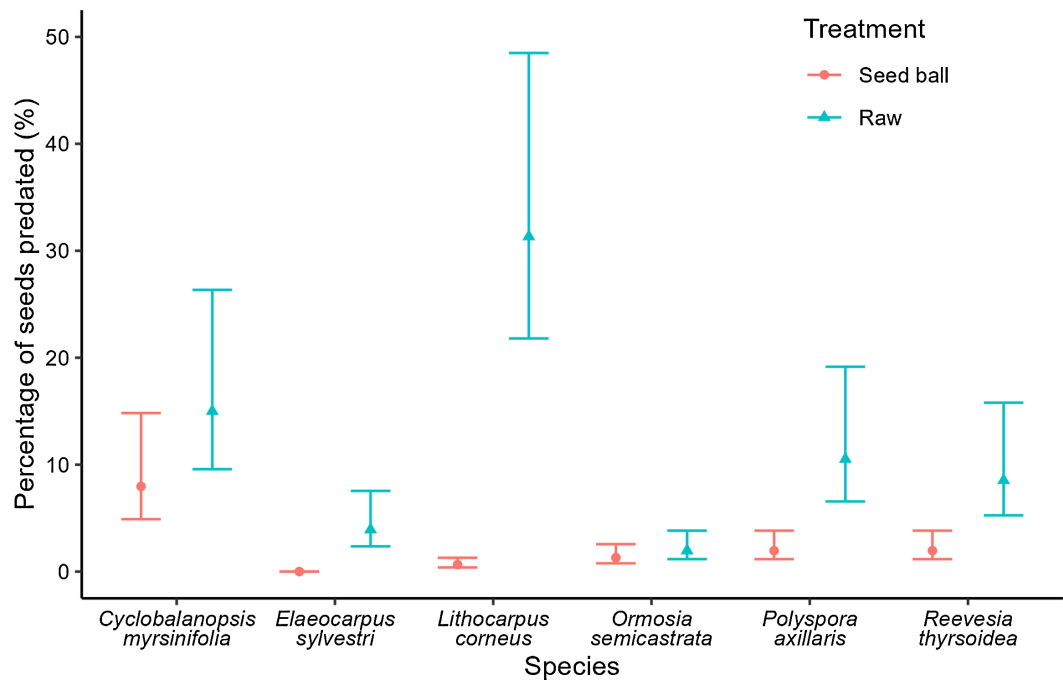


Figure 4. Differences in the percentage of seeds that are predated for each species and under different treatments. Error bars denote the 95% confidence intervals.

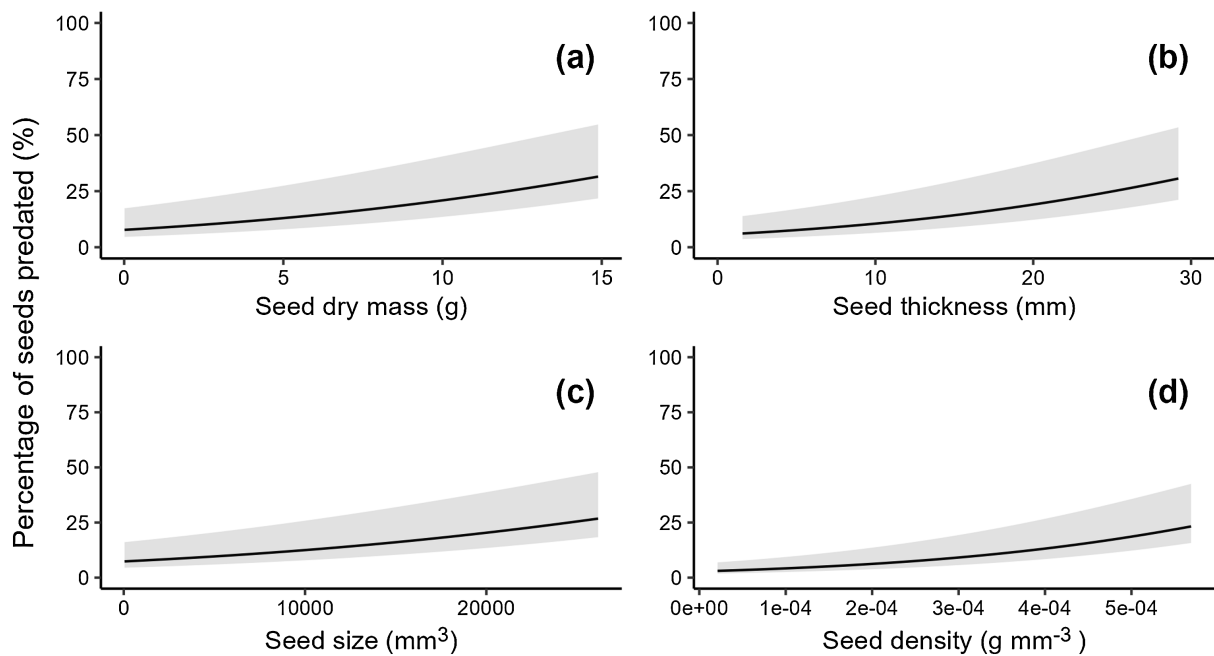


Figure 5. Percentage of seeds that were predated against (a) seed dry mass; (b) seed thickness; (c) seed size; and (d) seed density. Shaded regions represent 95% confidence intervals.

encrusted seeds at reducing seed predation, we found that average dry mass, average thickness, and average size all had significant interactions with how successful the seed balls were at reducing seed predation. Specifically, **Figure 6** shows that biochar-based encrusted seeds were increasingly effective at reducing predation

as their dry mass, thickness, and size increased. However, seed density did not have a significant interaction with the seed coat treatment.

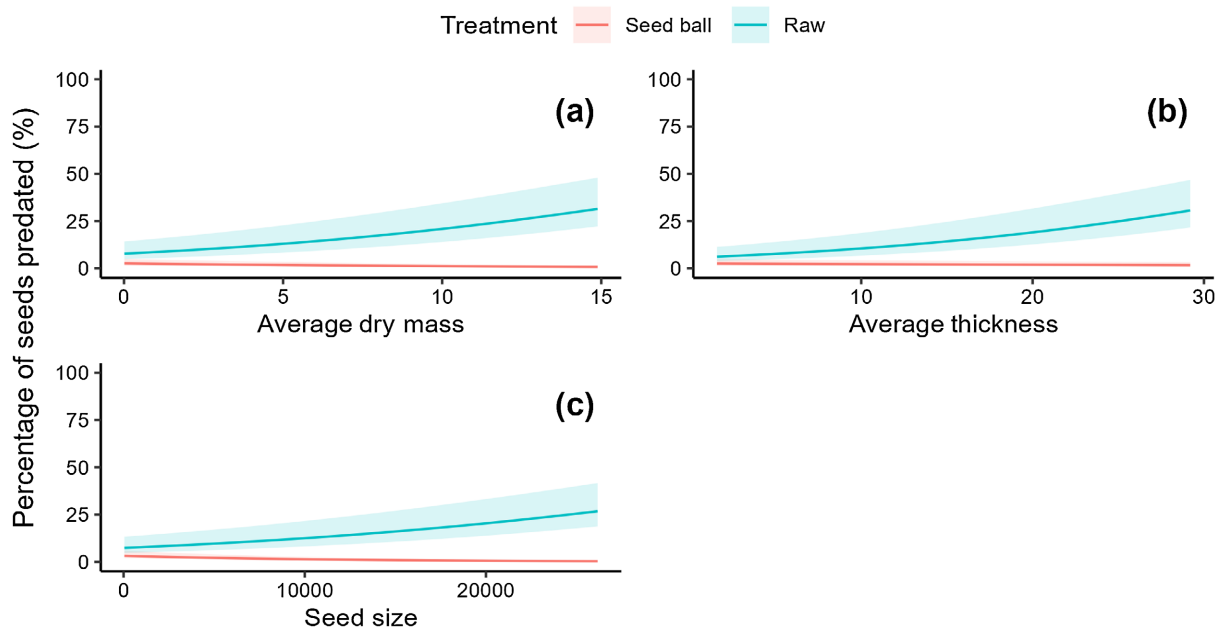


Figure 6. Percentage of seeds that were predated under two treatments against (a) seed dry mass; (b) seed thickness; and (c) seed size. Seed density was not included as the interaction was not significant. Shaded regions represent 95% confidence intervals.

For the global model that combined the datasets from both experiments, the best model included the three-way interaction. Within this model, we found that the different species had significantly different predation rates, but that the seed coat treatment itself was no longer a significant driver of predation rate. The experimental design itself was not statistically significant but had a low p-value of 0.062. Additionally, a significant interaction between experimental design and *Polyspora* was found, suggesting that this species was targeted differently by predators across the two experiments.

4. Discussion

As the importance of ecosystem restoration increasingly becomes recognised, methods to efficiently and effectively restore large areas of degraded landscapes are needed. Our study here has shown that applying a biochar-based coating to seeds before direct seeding can significantly reduce seed predation, thus increasing the number of seeds that can subsequently germinate and improving restoration results. Moreover, we found that the effectiveness of the biochar-based seed coats varied across different species. Across the six species included in our study, four species showed significantly fewer seeds that were predated when they were treated with biochar-based seed coats. The seed coat treatment was the most effective when applied to *L. corneus*, which had the highest predation rate across all species tested when left as raw seeds. When treated and sowed as biochar-based

encrusted seeds, almost none of the *L. corneus* seeds were predated.

For the two species in which biochar-based seed coating did not significantly reduce predation, *O. semicastrata* had very low predation rates even when left as raw seeds, suggesting that the granivores already had low preference to these seeds and thus the seed coats did not have much effect for this species. On the other hand, the biochar-based seed coating reduced the probability of *C. myrsinifolia* seeds being predated, but the difference was not statistically significant. This is also the only species where there was still a substantial proportion of seeds that were predated, even after the seeds were made into biochar-based encrusted seeds, suggesting a very high preference for seeds from this species by the granivores that was not significantly reduced with the biochar-based seed coat.

Focusing on the specific morphological traits that may affect seed predation rates and the effectiveness of biochar-based encrusted seeds in reducing predation, we found a significant positive relationship between dry mass, thickness, size, and density with the proportion of seeds predated, agreeing with previous studies (Maron et al., 2012; Foffová et al., 2020). At the same time, we also found the effectiveness of biochar-based seed coating to reduce predation, which also followed a similar relationship, where the biochar-based encrusted seeds were more effective as seed dry mass, thickness, and size increased. Notably, seed density did not have a significant interaction with the seed coat treatment. Biochar-based encrusted seeds may be able to behave similarly to the ash after wildfires, masking the scent of seeds and impair the olfaction of rodents (Briggs & Vander Wall, 2004; Taylor et al., 2020), which was previously shown as one of the most common seed predators on degraded hillsides in Hong Kong (Hau, 1997). Additionally, the alteration of the seeds' physical properties also likely increased handling time of the seeds by the granivores, decreasing their attractiveness. This behaviour has the potential to affect both rodents (Lawhon & Hafner, 1981) and wild boars (Davidson et al., 2022), the granivores commonly found in Hong Kong.

An unexpected result from our experiments is the difference in predation rate between the pilot and the main experiment. A potential explanation for the difference is the timing of the degradation, and thus soil condition between the two experiments (Van Eynde et al., 2017). For the main experiment, the date of the landslides that deforested the study sites was known and the study was conducted within three years of the landslide. However, the date of the land degradation for the pilot study areas was unknown and more time may have elapsed between degradation and restoration. Apart from soil condition, seed predation may also be affected by other factors, such as natural resource availability, provision of microhabitats, compositions of vegetation and weather variability (Mittelbach & Gross, 1984; Perez-Ramos & Marañón, 2008; Solbreck & Sillén-Tullberg, 1986).

In our experiment, *P. axillaris* and *R. thyrsoides* had the smallest seeds (<100 mm²) and both had their chance of being predated significantly lowered by the presence of the biochar-based seed coat. For these species, increased handling time is likely to have been one of the major reasons for the effectiveness of the

biochar-based seed coating (Jacobs, 1992). However, *L. corneus* seeds are already naturally quite large and thus the increase in handling time may have been less pronounced. Thus, the effectiveness of the biochar-based seed coat will likely be due to other reasons. However, to confirm the above hypotheses and test the specific mechanics of how the biochar-based seed coats deter granivores, further experiments will be needed. Given the different granivores that are present in Hong Kong, it is possible that multiple mechanisms are in play, where rodents are deterred by one reason, for example, increased handling time, while wild boars are deterred by another.

While our study suggests that applying a biochar-based seed coat is an effective means of reducing seed predation on landslide sites, it is important to note that in our study, all the seeds were placed and the potential granivores were effectively given a direct choice between raw seeds and biochar-based encrusted seeds. For real restoration applications, it is likely that all seeds will be sowed as biochar-based encrusted seeds on the restoration sites. In the event that no alternatives are given, it is possible that the effect of encrusting seeds in biochar reducing predation rates is diminished. Additional studies will need to be conducted to evaluate the effectiveness of biochar seed coating in these circumstances. Our study also showed that some species, such as *O. semicastrata*, have very low predation rate compared to the other seeds when present together within a seed tray; while other species, such as *C. myrsinifolia*, are relatively less affected by the biochar-based seed coating. Our experiment here was not able to explain these differences, and further experiments will be needed. For example, experiments with only *O. semicastrata* will be conducted to investigate whether granivores will predate these seeds when no other choices are available. Additional seed nutrient or physical properties analysis can also be done to investigate whether granivores are choosing seeds based on high nutrient content and/or ease of access due to seed shells.

5. Conclusion

As the importance of forest restoration continues to garner attention globally as an important tool to restore biodiversity and encourage sustainable development, cost-effective, efficient methods of restoration are needed. Direct seeding is increasingly advocated as a means to boost forest recovery, particularly when the target region covers a large area of difficult-to-access terrain (Law et al., 2023). Moreover, landslide scars are degraded landscapes that could benefit the most from successful forest restoration, restoring biodiversity while also stabilising the vulnerable slopes from further landslides and disturbance (Pang et al., 2018). While seed predation presents a challenge to successful forest restoration, our results show that applying a biochar-based seed coat is able to significantly reduce the predation rate of most of the native species we have tested in this study, almost reducing predation rates to zero for five of the six tested species within a subtropical urban environment. Combined with its effectiveness at increasing seed germination in these degraded landscapes (Law et al., 2023), biochar-based seed

coating can be an effective method of boosting forest restoration success, helping seeds overcome two of the biggest obstacles they face, seed predation and low nutrient availability, when sowed directly on degraded soil.

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Data Availability

The data will be available on the University of Hong Kong data repository upon publication.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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Appendix

Table S1. List of all plant species within a 10 m buffer of the study area in the pilot experiment.

Study site	Scientific name	Family	Type
	<i>Ilex asprella</i>	Aquifoliaceae	Shrub
	<i>Schefflera heptaphylla</i>	Araliaceae	Tree
	<i>Casuarina equisetifolia</i>	Casuarinaceae	Tree
	<i>Aporosa dioica</i>	Euphorbiaceae	Tree
	<i>Bridelia tomentosa</i>	Euphorbiaceae	Shrub
	<i>Mallotus paniculatus</i>	Euphorbiaceae	Tree
Tsing Yi	<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>	Lauraceae	Shrub
	<i>Acacia confusa</i>	Mimosaceae	Tree
	<i>Corymbia citriodora</i>	Myrtaceae	Tree
	<i>Syzygium jambos</i>	Myrtaceae	Tree
	<i>Raphiolepis indica</i>	Rosaceae	Shrub
	<i>Psychotria asiatica</i>	Rubiaceae	Shrub
	<i>Polyspora axillaris</i>	Theaceae	Tree
	<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>	Lauraceae	Shrub
	<i>Melastoma sanguineum</i>	Melastomataceae	Shrub
Sham Tseng	<i>Rhodomyrtus tomentosa</i>	Myrtaceae	Shrub
	<i>Raphiolepis indica</i>	Rosaceae	Shrub
	<i>Polyspora axillaris</i>	Theaceae	Tree
	<i>Cratoxylum cochinchinense</i>	Clusiaceae	Tree
	<i>Mallotus paniculatus</i>	Euphorbiaceae	Tree
	<i>Dicranopteris pedata</i>	Gleicheniaceae	Fern
Ha Fa Shan	<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>	Lauraceae	Shrub
	<i>Rhodomyrtus tomentosa</i>	Myrtaceae	Shrub
	<i>Baeckea frutescens</i>	Myrtaceae	Shrub

Table S2. List of all plant species within a 10m buffer of the study area in the main experiment.

Study site	Scientific name	Family	Type
	<i>Blechnum orientale</i>	Blechnaceae	Fern
	<i>Mallotus paniculatus</i>	Euphorbiaceae	Tree
Kam Tin	<i>Macaranga tanarius</i> var. <i>tomentosa</i>	Euphorbiaceae	Tree
	<i>Dicranopteris pedata</i>	Gleicheniaceae	Fern
	<i>Trema orientalis</i>	Ulmaceae	Shrub
Ta Shek Wu	<i>Rhus succedanea</i>	Anacardiaceae	Shrub

Continued

	<i>Blechnum orientale</i>	Blechnaceae	Fern
	<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>	Lauraceae	Shrub
	<i>Melastoma malabathricum</i>	Melastomataceae	Shrub
	<i>Rhodomyrtus tomentosa</i>	Myrtaceae	Shrub
Sandy Ridge	<i>Blechnum orientale</i>	Blechnaceae	Fern
	<i>Macaranga tanarius</i> var. <i>tomentosa</i>	Euphorbiaceae	Tree
	<i>Breynia fruticosa</i>	Euphorbiaceae	Shrub
	<i>Rhodomyrtus tomentosa</i>	Myrtaceae	Shrub

Table S3. Plant species of seeds selected for experiments and their characteristics^a.

Experiment	Species	Family	Seed size (cm)	Dispersal mode	Successional stage
I & II	<i>Lithocarpus corneus</i>	Fagaceae	2.5 - 4.5	Animals	Late
	<i>Cyclobalanopsis myrsinifolia</i>	Fagaceae	1.5 - 2	Animals	Late
	<i>Polyspora axillaris</i>	Theaceae	0.5 - 1	Wind	Pioneer
II	<i>Reevesia thyrsoidea</i>	Sterculiaceae	0.5 - 1	Wind	Pioneer
	<i>Ormosia semicastrata</i>	Fabaceae	1	Animals	Late
	<i>Elaeocarpus sylvestris</i>	Elaeocarpaceae	2 - 2.5	Animals	Late

^aData are from Hong Kong Herbarium (2022), Meng et al. (2011), Tang & Ohsawa (2009), Hong Kong Wetland Park (2022), Mott MacDonald (2014) and Law et al. (2023).

**Figure S1.** Model YX-65 Sweet rice ball forming machine used to create biochar seed balls for *L. corneus*, *C. myrsinifolia* and *E. sylvestris*.