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REVIEW

A Review of the Engineering Role of Burrowing Animals: Implication of Chinese Pangolin as an Ecosystem Engineer

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ABSTRACT

Ecosystem engineers are organisms that alter the distribution of resources in the environment by creating, modifying, maintaining and/or destroying the habitat. They can affect the structure and function of the whole ecosystem furthermore. Burrowing engineers are an important group in ecosystem engineers as they play a critical role in soil translocation and habitat creation in various types of environment. However, few researchers have systematically summarized and analyzed the studies of burrowing engineers. We reviewing the existing ecological studies of burrowing engineer about their interaction with habitat through five directions: (1) soil turnover; (2) changing soil physicochemical properties; (3) changing plant community structure; (4) providing limited resources for commensal animals; and/or (5) affecting animal communities. The Chinese pangolin (*Manis pentadactyla*) is a typical example of burrowing mammals, in part (5), we focus on the interspecific relationships among burrow commensal species of Chinese pangolin. The engineering effects vary with environmental gradient, literature indicates that burrowing engineer play a stronger role in habitat transformation in the tropical and subtropical areas. The most common experiment method is comparative measurements (include different spatial and temporal scale), manipulative experiment is relatively few. We found that most of the engineering effects had positive feedback to the local ecosystem, increased plant abundance and resilience, increased biodiversity and consequently improved ecosystem functioning. With the global background of dramatic climate change and biodiversity loss in recent decades, we recommend future studies should improving knowledge of long-term engineering effects on population scale and landscape scale, exploring ecological cascades through trophic and engineering pathways, to better understand the attribute of the burrowing behavior of engineers to restore ecosystems and habitat creation. The review is presented as an aid to systematically expound the engineering effect of burrowing animals in the ecosystem, and provided new ideas and advice for planning and implementing conservation management.

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1. Introduction

Ecosystem engineers can influence resource availability for other species by modifying, maintaining or creating habitats [1]. It has been more than 20 years since the concept of ecosystem engineers was defined [2]. During this time, researchers have found strong evidence that ecosystem engineers play a pivotal role in the habitat. Contemporary studies about ecosystem engineers focus on their impacts on soil physicochemical property and vegetation community structure and, increasingly, on their potential as agents of ecosystem restoration.

Research on ecosystem engineering covers many species and themes. Coggan (2017) collected 214 articles covering the interactions of 121 engineering species across four taxa (mammals, reptiles, birds, invertebrates). The most observed types of ecosystem engineers in mammals are the burrowing ones, and they can have large impacts on the other species, environments, and ecological processes [3]. Burrowing activity is an important form of natural disturbance in many types of ecosystems, existing evidence suggests that the burrows of these engineers has profound effects on shaping the abiotic environment, leading to the integrity of the biotic community [4,5]. By creating discrete patches of disturbance, burrowing engineers can increase abiotic heterogeneity at the landscape level, generating novel microhabitats, as described in previous studies on the burrow function of aardvarks (*Orycteropus afer*), warthogs (*Phacochoerus aethiopicus*) and Cape porcupines (*Hystrix africaeaustralis*) [6,7,8]. However, the ecology research of other burrowing animal still lacking these insights, meanwhile, there are not enough review papers to summarize the studies of burrowing engineers and provide suggestions for current hot issues and future research directions.

To explore the roles played by burrowing engineers in their habitat, we searched the key terms such as “Chinese pangolin”, “burrowing engineers”, “soil disturbance”, “biodiversity”, “biogeomorphology”, and “soil turnover”, and filtered these papers with the limit of “burrowing animal” to identify papers about burrowing engineers. By using the database compilation method, 117 papers were documented and 65 papers were selected as represents of engineer species (Table 1). We found that since the concept of ecosystem engineer was put forward, the number of studies related to burrowing engineers has been on the rise, indicating that the ecological function of burrowing engineers has been paid more and more attention by the researchers (Figure 2). We classified the known ecological functions of burrowing engineers in the literature into five directions: (1) soil turnover; (2) changing soil physicochemical properties; (3) changing plant community structure; (4) providing limited resource about open microsites, shelters, thermal refuges and food for commensal animals; and (5) affecting animal communities (Figure 1).

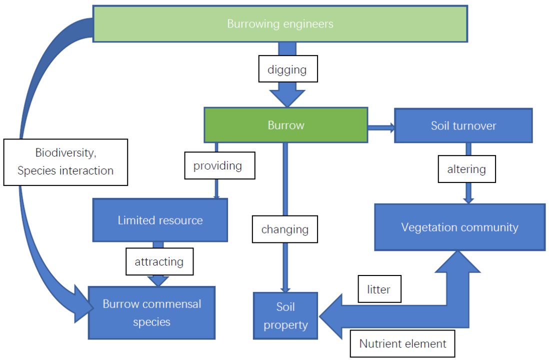

Figure 1. Research framework of burrowing engineers.

Burrowing engineers digging burrows for foraging or dwelling, removing big amounts of sediment from deep layer to surface in this process, generated soil turnover (1), changed soil physicochemical property, too (2). On the one hand, soil turnover firstly altering the vegetation community structure, due to the change of physicochemical properties of burrow soil, the vegetation community is continuously affected (3); On the another

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hand, burrow providing limited resource such as shelter, thermal refugia, food resource, mating site … (4). Other species are attracted by abundant resource from burrowing and forming a burrow commensal population, and their interaction affected ecosystem biodiversity (5). In addition, the soil physicochemical property is also affected by plant litter decomposition (2).

Research contents: Summarize the content of the

Table 1. The studies of burrowing engineers

Species	Research contents	Enviroment	Positive/ negative	Reference
(*Myrmica rubra*) / (*asius niger*)	B, E	grassland	Positive/ negative	[133]
Aardvark (*Orycteropus afer*)	B, C	grassland, savannah, arid scrubland	negative	[21]
African ice rat (*Otomys sloggetti robertsi*)	A, D	alpine meadow	Positive	[134]
Arctic foxes (*Vulpes lagopus*)	B	grassland,woodland	Positive	[135]
Badgers (*Meles meles*)	B, C	shrub-steppe/annual grasslands	Positive	[86]
Badgers (*Meles meles*) and foxes (*Vulpes vulpes*)	B, C	European temperate forest	Positive	[64]
Banner-tailed kangaroo rat (*Dipodomys spectabilis*)	B	creosote bush shrubland	neutral	[136]
Bare-nosed wombat (*Vombatus ursinus*)/cattle (*Bos taurus*)	A	floodplains and terraces	Positive	[13]
Bear (*Ursidae*)	A, B	Alpine	neutral	[137]
Beaver (*Castor canadensis*)	E	Wetlands	Positive	[138]
Black-tailed prairie dog (*Cynomys ludovic-ianus*)	D, E	grassland(arid)	Positive	[139]
Burrow-dwelling tortoises (*Gopherus polyphemus*)	D	coastal dune ecosystem	Positive	[93]
Burrowing bettong (*Bettongia lesueur*)	B, C	woodland	Positive/ negative	[50]
Burrowing crab (*Helice tientsinensis*)	A, B	intertidal salt marsh	Positive	[24]
burrowing seabirds	B, C, E	secondary forest	Positive	[140]
Camel spider (*Arachnida, Solifugae*)/Black-tailed prairie dogs (*Cynomys ludovicianus*)	C, E	grassland(arid)	Positive	[141]
Cape ground squirrels (*Xerus inauris*)	C, E	Namib Desert grasslands	Positive/ negative	[28]
Cape porcupines (*Hystrix africaeaustralis*)	A, D	semi-arid environment	Positive	[4]
Common vole (*Microtus arvalis*)/European mole (*Talpa europaea*)/ earthworm (Lumbricus terrestris)	B	floodplain	Positive	[142]
Earthworm (Lumbricus terrestris)/salamander (*P. glutinosus*)	D, E	forest is mixed deciduous	Positive	[143]
Eastern barred bandicoots (*Perameles gunnii*)	A	woodland and grassland	neutral	[18]
Eastern bettong (*Bettongia gaimardi*)	A, B	grassy woodland	Positive	[144]
Eastern bettong (*Bettongia gaimardi*) /European rabbit (*Oryctolagus cuniculus*)	B, C, D	grassland/woodland/forest	neutral	[145]
Eastern bettongs (*Bettongia gaimardi*)/short-beaked echidnas (*Tachyglossus aculeatus*)	A, B	forest	Positive	[25]
Eurasian badger (*Meles meles L.*)	A	woodland	neutral	[14]
European bee-eater (*Merops apiaster*)	A, E	arid desert environments	Positive/ negative	[16]
European ground squirrel (*Spermophilus citellus*) /spider (*Araneae*)/ harvestman (*Opiliones*)	E	Grassland	Positive	[146]
European rabbit (*Oryctolagus cuniculus*)	C, E	Grasslands	Positive	[33]
Fat sand rats (*Psammomys obesus*)	A.C	desert/shrub(arid)	negative	[127]
Fossorial rodent (*Parotomys brantsii*)	B, C	Desert	Positive	[55]
Giant armadillo (*Priodontes maximus*)	C, D, E	dry forest plains	Positive	[108]
Giant kangaroo rat (*Dipodomysingens*)	C	semiarid annual rangeland	negative	[129]
Gopher Tortoise (*Gopherus polyphemus*)	A	pine forest,scrub	neutral	[27]

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Species	Research contents	Enviroment	Positive/ negative	Reference
Harvester ants (*Messor barbarus*)	B, C	Mediterranean grassland	Positive	[35]
House mouse (*Mus musculus*)	A	limestone island	negative	[12]
Indian crested porcupine (*Hystrix indica*)/harvester ants (*Messor spp.*)	C, E	desert	Positive	[147]
Kangaroo rats (*Dipodomys spectabilis*)	B, C	arid grassland	Positive	[148]
Lamprey larvae (*Eudontomyzon sp.*)	B, E	river substrates	Positive	[149]
Liberian mongoose (*Liberiictis kuhni*)	C	lowland rain forest	Positive	[150]
Malleefowl (*Leipoa ocerlata*)/bumowing bettong (*Bettongia lesueur*)	B, C	semi-arid woodland	Positive	[151]
Marsh crabs (*Sesarma reticulatum*)	A	salt marshes	negative	[126]
Mole-rats (*Bathyergidae*)	B, C	grassland	Positive	[152]
Mycophagous woylie (*Bettongia penicillata ogilbyi*)/omnivorous quenda (*Isoodon fusciventer*)	C, E	mesic forest	Positive	[31]
Nine-banded armadillos (*Dasypus novemcinctus*)	A	forest	neutral	[11]
Pikas (*Ochotona curzoniae*)	B	alpine grasslands	neutral	[26]
Plains vizcachas (*Lagostomus maximus*)	B	shrub	Positive	[153]
Plateau zokors (*Myospalax fontanierii*)	B, C, E	alpine meadow ecosystems	Positive	[154]
Pocket gopher (*Thomomys talpoides*)	B, C	grassland	neutral	[155]
Prairie dogs (*Cynomys gunnisoni*)/ kangaroo rats (*Dipodomys spectabilis*)	B, C, E	Desert grassland	Positive	[156]
Prairie dogs (*Cynomys ludovicianus*)	B	Semiarid Grasslands	Positive	[157]
Pygmy rabbit (*Brachylagus idahoensis*)	B, C	high-elevation sagebrush steppe	Positive	[158]
Rabbit (*Oryctolagus cuniculus L.*)	B, C	Australian semiarid woodland	negative	[125]
Red fox (*Vulpes vulpes Linnaeus*)	B, C	grasslands, wetlands, alkaline marshes.	Positive	[62]
Relic bilby (*Macrotis lagotis*)	B, C, D	woodland	Positive	[48]
Richardson's ground squirrel (*Urocitellus richardsonii*)	B, C	open grassland	Positive	[159]
Short-beaked echidna (*Tachyglossus aculeatus*)	A, C	semi-arid woodlands	Positive	[160]
Sooty shearwaters (*Puffinus griseus*)	A, B	woods	neutral	[161]
Southern brown bandicoot (*Isoodon obesulus*)	B, C	forest	Positive	[38]
Tatra marmots (*Marmota marmota latirostris*)	B, C	alpine meadow	Positive	[32]
Termites/ants/earthworms	B, C, E		Positive	[162]
Trapdoor (*Mygalomorphae*) spiders/Pygmy bluetongue lizards (*Tiliqua adelaidensis*)	E	semi-arid native grassland	Positive	[163]
Tuco-tuco (*Creilomjs fnlnmnz*)	B, C	natural coastal grassland	Positive	[34]
Water voles (*Arvicola amphibious*)	C	wet grassland	neutral	[164]
Wedge-tailed Shearwaters (*Puffinus pacificus*)	C	limestone island	negative	[165]
Woylie (*Bettongia penicillata*)	A	woodland	Positive	[40]

selected articles and divide them into five directions as is described above.

Due to the continuously loss of global biodiversity, burrowing engineers will play an increasingly important role in biodiversity conservation, because of their unique attribute to increase the heterogeneity of habitats and provide limited resource for other biological communities. The function of engineers will promote interspecific connections and increase environmental capacity. For the conservation of burrowing engineers, we should recognize that the rejuvenation of their population may also benefit other species to achieve double the result with half the effort. Conversely, the extinction of engineers is likely to cause a chain of ecological losses. In this article, we provide a better understanding of the interaction among burrowing engineers with local habitats and also discussed

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the composition and interspecific relationship of Chinese pangolin commensal species.

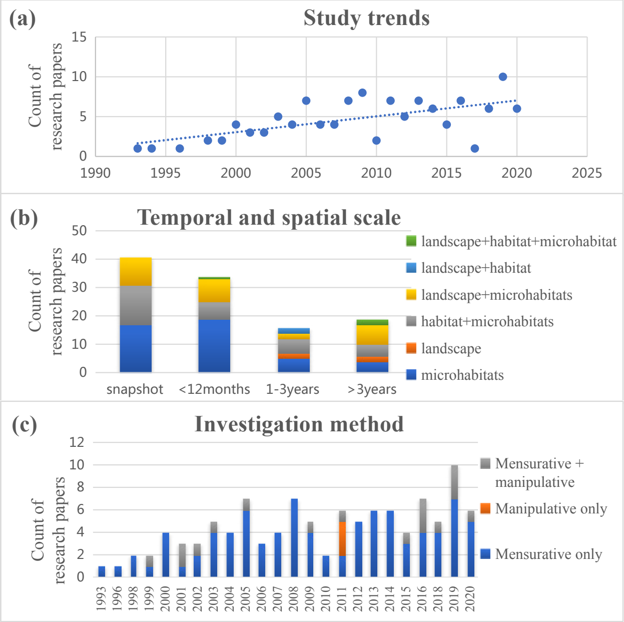

Figure 2. Trends in the methods used to study burrowing engineering. (a) The counts of research papers published on burrowing engineers, (b) Temporal and spatial scale of experiments performed and (c) the investigation method of field observations

2. Engineering Role of Burrowing Animals in Ecosystems

The unifying idea of the studies we identified is that burrowing activity is an important form of natural disturbance in many ecosystems as it increases habitat heterogeneity and improves the living conditions of some species [4,5]. We briefly discuss the ecological function of burrowing engineers from five directions, introduce the major findings and flaws in these research fields and propose some suggestions for further research.

We found that the dominating experiment method of burrowing engineers research is comparative measurement, rather than manipulative experiment (Figure 1). These studies explored the ecological function of burrowing engineers by comparing soil properties, plant community structure between disturbed and undisturbed areas. Pringle once said that manipulative studies have greater utility in identifying the driving mechanisms behind the impacts of engineers than measurement studies because they require the elimination of competing hypotheses by controlling sources of variation [9]. The probable reason may be the manipulative experiment is difficult to implement and the environmental interference is difficult to eliminate. On the contrary, the difficulty in experimental design and operation of comparative measurement is lower, and the statistical results of data are more accurate.

2.1 Soil Turnover by Engineers

Burrowing activity causes the massive amounts of soil been turnover, directly modifies the habitat geography.. The burrowing activity usually serves two purposes: dwelling and foraging, or both (as for the pangolin). The degree of soil turnover of burrowing animals mainly depends on their body size and morphological traits. In some regions, burrowing animals are thought to be the dominant geomorphic agents, displacing more sediment through their burrowing than all other abiotic processes combined [10]. Many researchers have measured the volume/quality of removed soil to quantify this activity, which has major effects on ecosystems. The morphological volume of burrow calculated by two methods: One is measure burrow tunnel size (think of them approximately as regular three-dimensional structures, such as cylinders and cones [11,12], the another one is measure soil mound size [13,14]. The mass is converted from volume × density. Then, by multiplying the average soil transport volume of a single burrow by the excavation frequency or the density of the burrow, the soil transport volume of the target population can be roughly estimated and the ability of the engineer to physically modify the surface topography can be quantified [15,16,17,18]. For instance, the European bee-eater (*Merops apiaster*) was conservatively estimated to move 8.71 L of sand during the construction of nests, which equals to 12.94 kg of sand. Sixty-seven nests were dug during the 3 study years, amounting to approximately 583 L or 867 kg. In addition, because all the nests were on a cliff, four large pieces collapsed from the cliff during the study period, amounting to 3064 L or 4554 kg [16]. In the semiarid regions of Western Australia, rush-tailed bettongs (*Bettongia penicillata*) and southern brown bandicoots (*Isoodon obesulus*) can turnover 4.8 and 3.9 tonnes of soil annually, respectively [15,17].

At present, the burrow volume measurement methods used in relevant soil turnover studies can only be used for rough estimation, but cannot obtain accurate volume values. When this value is applied to the physical modification of the geography of the quantitative population, a large deviation will occur. Some researchers have tried to measure the burrow volume more accurately through mathematical modeling [19]. Therefore, how to simplify this method and successfully apply it to related researches is a difficult problem that needs to be solved at present. In addition, the soil removement by engineers should be combined with its population size, and the biogeographical function of burrowing engineers should be discussed at the landscape level.

2.2 Burrowing Engineers Changes Soil Physicochemical Properties

Bioturbation of engineers contributes to soil mainly via mechanical turnover by excavating deep soil to the surface and burying the original surface organic matter underground. Researchers detected soil samples to obtain physicochemical property data, such as moisture, temperature, compaction, hydrophobicity, ammonium nitrogen, conductivity, distribution of litter and the present all kinds of trace elements in the soil. In this part, we mainly discuss the experiment methods and the result of burrowing engineer changes soil physicochemical properties.

2.2.1 Comparative Measurement for Soil Physicochemical Properties

In order to explore the engineering effect on soil physicochemical properties, researchers usually compared soil property between disturbed and undisturbed surfaces. Mallen-Cooper et al (2019) quantitatively synthesised the findings of 149 published studies that compared disturbed and undisturbed soil surfaces, included 64 engineer species, but not all burrowing engineers [20]. We discuss the application of comparative measurement methods in this kind of research on different spatial and temporal scales, divide the spatial scale into three categories: microsite (less than 5 m or 5 m^2), habitat (up to 1 km or 100 ha) and landscape scale (more than 1 km or 100 ha); divide the temporal scale into four categories: snapshot, <12 months, 1-3 years and >3 years (Figure 1).

At the microhabitat scale, researchers commonly detected soil samples from different microsites at each burrow (inside, the entrance of burrow, excavated mounds, undisturbed sites, etc.) to compare engineering effect on soil properties [21,22,23,24]. In addition, some researchers furtherly add artificial burrows as a control group to highlight the unique changes in the soil properties caused by animal digging. For example, Qiu et al (2019) selected three sample plots, artificial conburrow-convex microtopography, natural conburrow-convex microtopography generated by crab burrows and natural flat microtopography with few or no crab burrows, and then compared the differences in the soil carbon and nitrogen content indices [24].

At the habitat and landscape scales, bioturbation is affected by different environmental factors, including plant type, precipitation (different degrees of drying), altitude, etc., they are selected as concomitant variables to quantify the interaction between environment and burrowing engineers [21,25,26,27,28]. Davies et al (2019) distinguished three plant types in Tasmanian temperate woodlands, and they detected soil fertility and structure to explore the different effects of burrowing engineers on soil. These effects on soil fertility and structure were strongest in habitats with dry and poor soil [25]. Burbidge et al (2007) detected the difference in soil physicochemical properties between the burrow mounds and the undisturbed areas at the landscape scale, and they found the soil penetrability typically at mounds far greater than surrounding soil that often has a hard pan [29].

More studies have used methods that measure and compare soil physicochemical properties at multiple spatial scales between disturbed and undisturbed areas. For instance, comparative measurement of soil properties in combination with microhabitats scale at the landscape scale [19,30,31,32,33]; and combination with microhabitats scale at the habitat scale [14,24,29,34,35]; and combination with habitat scale at the landscape scale, but few studies were used this method [36,37]. In general, the studies based on the combination of multiple spatial scales have become more popular. Compared with a single-scale measurement, the multi-scale experimental methods can reveal the influence of burrowing engineers on soil properties more comprehensively and deeply.

The studies about engineering effect on soil property usually compare and measure property at temporal scale. There is a typical study, in Australia, the southern brown bandicoot (*Isoodon obesulus*; Peramelidae) leaves foraging pits after eating, and fresh diggings typically contain a higher moisture content and lower hydrophobicity than undisturbed soil. One month later, the soil fertility is increased, so researchers speculated the reason may be the foraging pits accumulated more organic materials than undisturbed areas [38]. However, the soil physicochemical properties don't regularly change linearly with time. For example, the soil permeability in fresh foraging burrows of Chinese pangolin will increase because the hardened topsoil is destroyed. With the accumulation of organic matter and the formation of a new waterproof layer, the soil permeability begins to decline. However, the accumulation of organic matter increased soil fertility, which was beneficial to the development of soil organisms and plant colonization (unpublished data). The burrows created by engineers are characterized by legacy effects because of their persistence. In fact, the burrows of autogenic engineers like pangolins and aardvark (*Orycteropus afer*) often persist long after the organism's death (Hastings et al, 2007). Consequently, the understanding of the soil property transformation in an entire burrow cycle (from dig to collapse) is necessary. However, the literature shows the

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most studies only compare and measure soil properties in different areas at the snapshot scale (Figure 1). Long-term monitoring of changes in soil physicochemical properties is still lacking. One method is to compare soil properties of new and old burrows at the same time [21, 38], meanwhile, the environment character and disturbance level of burrows in different ages are supposed to be similar.

2.2.2 Engineering Effect on Soil Property is Vary with Environment Gradient

Considerable studies about the engineering effect on soil property caused by burrowing engineers have concentrated on arid and semiarid environments (Figure 3) [4,39,40,41,42,43,44]. More evidence has demonstrated that engineering effect is stronger in arid and semiarid regions than in mesic and semi-mesic regions [25,38]. This may be due to increased water infiltration (moist soil excavated by engineers) in xeric environments which may make a substantial difference in plant survival and growth, as soil nutrients are more easily absorbed when in solution [45]. In contrast, the high initial soil moisture in mesic environments leaves little opportunity for moisture to be further increased. Another potential reason for this difference in bioturbation is that in arid and poor soil habitats, large amounts of nutrients are lost from top layer soil (heat and weathering, etc.), while subsoil is relatively fertile and rich in certain trace elements [46].

We can reasonably speculate that pangolins would increase soil moisture, consistent with similar disturbances made by aardvark (*Orycteropus afer*), echidna (*Tachyglossus aculeatus*) in other systems [41,47], and decrease soil compaction, similar to the effects of bilby (*Macrotis lagotis*), echidna (*Tachyglossidae*) and brush-tailed bettong diggings (*Bettongia penicillata*) [21,41,47,48]. Meanwhile, Chinese pangolins are mainly distributed in mesic and semi-mesic regions, and much less is known about the role of burrowing species play in mesic environments.

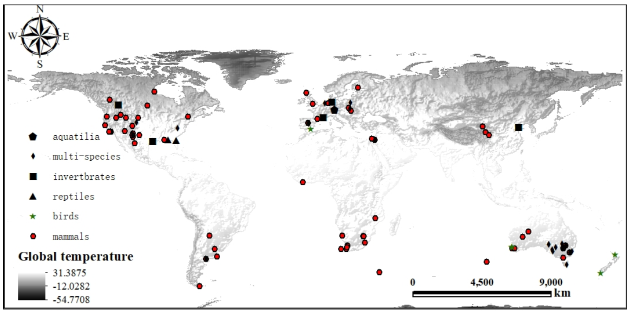

Figure 3. Global distribution of burrowing engineers research. Points on the map represent the type of engineering species by shape and colors. The proportion of all kinds of burrowing engineers.

2.3 Burrowing Engineers Change Plant Community Structure

Engineers play an important role in the local ecosystem and affect plant community structure with two ways: by directly foraging for individual plants and vegetation communities (trophic effects) and by unique bioturbation (burrowing), which can affect soil properties and indirectly influence vegetation. Changes in soil properties as a direct result of bioturbation by burrowing engineers and generate distinct patterns of plant community composition and diversity, which are enhanced by the indirect effects of engineered soil properties on the productivity, biomass and growth rates of plant species [49]. Previous studies have explored the roles of burrowing engineers in affecting plants structure by measuring and comparing seedbanks and plant structures in the presence and absence of burrow, respectively.

2.3.1 Burrows and Mounds Change the Vegetation Seedbank

Burrowing engineers affect seed banks, mainly reflected in seed aggregation and seed germination [50,51]. Valentine et al considered the reason for the preferable seed aggregation effect in disturbed pits because i) the undulating surface heterogeneity (caused by diggings) reduces seed removal by wind or seed predators, ii) the diggings collapsed and slightly buried seeds and hence protected them [38]. These hypotheses are also expressed in other related studies [21,31,35]. These studies tested their hypotheses by gathering seeds in soil from disturbed and undisturbed areas to highlight the otherness between sampling points. For example, more seeds are accumulated in mounds constructed by kangaroo rats (*Dipodomys spectabilis*) [52], bilby (*Macrotis lagotis*) [53] and bettong (*Bettongia lesueur*) [54] than in undug adjacent soils.

The mechanical turnover of soil by burrowing engineers can increase soil moisture and bury organic matter, bringing it in close contact with soil microorganisms and thereby altering soil microbial activity and litter decomposition [41,43,55,56]. Engineered soil enhances seed germination under laboratory conditions, too [38,57]. Some researchers seeded five endemic species in artificial foraging pits (imitating the natural foraging pit, as the physicochemical properties of soil are basically similar), spoiled heaps and the undug surface and then the number of each germinated seed at each site during the next 18 weeks are recorded. They found that the presence of artificial pits contributed to greater seedling recruitment for

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three of the plant species tested and seed germination at artificial foraging pits was generally higher than at other sites [38].

The soil property changed by burrowing engineers may depress germination of some species over others, too. Particularly in drier habitats, bioturbation has brought about more significant changes in soil physicochemical properties. The content of some trace elements will change greatly. Canals et al. (2003) has reported 10-fold higher nitrate concentrations on pocket gopher mounds in an annual California grassland, excessive nitrate inhibits seed germination [58,59,60].

2.3.2 Burrow Changing the Vegetation Community Structure

Burrowing activity is a process that manufactures pioneer microhabitats, adding habitat heterogeneity and creating a small area of open habitat (soil heap). Novel plant communities invade and colonize in this open area of the habitat, which leads to secondary succession of the ecosystem. The combination of a consistent soil disturbance and an altered soil nutrient concentration promotes the growth or hinders the recruitment of some plant species, an important driver of plant assemblage succession [61].

To reveal the effect of fox burrowing behavior on plant community structure, researchers conducted a plant sample survey (50 × 50 cm plots on the surface of the fox burrow and in the adjacent dry grassland) and recorded the percentage cover of all vascular plant species and the thickness and percentage cover of the litter layer in each plot [62]. They found i) a high proportion of nutrient-demanding species on fox burrows; ii) that the total species richness was lower on the burrows than in grasslands; and iii) that the total species richness was also lower in cleared areas (surrounded by cropland) than in complex landscapes (surrounded by more than 20% dry grasslands and a low proportion of arable lands within a radius of 200 m). These findings suggested that open microsites provided by the soil heap supported the encroachment of vanguard species due to the decreased level of competition [63], increased or changed nutrient availability [64,65] and reduced the amount of litter [66,67].

During the succession, Paschke et al (2000) considered the slower-growing perennials become dominant when nutrient uptake by early-seral species can no longer support their rapid aboveground growth [68]. Godó et al (2018) also recognized this point because after persistent observations, they found that tussock-forming grass species were particularly successful in recolonization due to their robust physiognomy and higher competitive ability [62,69]. Based on this phenomenon, they believed that despite the recent disturbance causing a temporal local encroachment of noxious species, patches of disturbed surfaces can be overgrown by specialist species [70]. The pangolin burrow consists of two parts: the burrow tunnel and the soil mound outside the burrow (see Figure 4).

Figure 4. The appearance of the pangolin burrow, including the tunnel and the mound outside the burrow: (a) and (b) are new burrows that are less than one year old, (c) and (d) are old burrow that are more than one year old.

The soil excavated from deep layer covers the surface outside the burrow mouth and turns the area into bare ground, and mound covers an area from 0.12 square metres to more than 2.98 square metres (unpublished data). We believe that pangolin bioturbation affects plant community succession because the spoil heap buries the old plant community and creates an open microhabitat for the establishment of new vegetation species. In our field investigation of the Chinese pangolin, the variation trend of the plant community structure surrounding the burrow consistent with Paschke's consideration by observing and comparing different burrows with different ages. We made a 2×2 m herb quadrant and a 5×5 m shrub quadrant centred on the burrow and randomly selected two undisturbed areas within a radius of 15 m around the burrow to produce same quadrants. We found that the difference of plant community structure on the fresh mound and the undisturbed area was the greatest. The older the burrow was, the smaller the difference was. When the burrow collapsed and the mound disappeared due to trampling and rain erosion, the plant community on the mound also evolved to the highest level, similar to the plant community structure in an undisturbed area (unpublished data).

The survey area of pangolin is mainly concentrated in humid mountainous and hilly areas. The bioturbation caused by pangolins may have a transient effect on plant community structure, with shrubs and trees already growing on most of the abandoned old burrows and mounds, which may be due to the abundant rainfall and fertile soil (rapid decomposition of litter) in this area, promoting the growth and breeding of plants. In drylands, soil disturbance by burrowing engineers has shown stronger effects on plant community structure [21,63,71,72,73]. We speculate that this phenomenon mainly occurs because drier regions exhibit more landscape unicity than wetter regions, which reveals the vital ecological function of burrowing engineers. Because engineers excavated deep soil rich in water and nutrients out of the ground to form mound, vanguard species are first planted due to their rapid growth and high nutrient requirements. Meanwhile, the naturally low rate of litter decomposition and the plant recruitment characteristics of arid and semiarid environments limit plant growth in undisturbed areas [74,75]. Research on the leaf litter decomposition rate, seed bank recruitment and success, and germination should be long-term to detect continuous changes in vegetation structure. Meanwhile, engineers can be herbivores, and the net effect of engineer foraging can have significant impacts on plant community structure [44,76]. However, there is a lack of relevant studies, and more attention should be paid to these engineers in future research.

2.4 Burrow Providing Limited Resource for Commensal Species

The burrows created by burrowing engineers has the characters as sturdiness, concealment, structural complexity, persistence et al. We summarized the types of burrow resources in relevant literature, including: spawning site, shelter, thermal refugia, foraging grounds. In addition, we have observed pangolin burrows as mating sites and natural toilets for other animals, but lack of strong evidence to support this, so we will not discuss it here.

2.4.1 Commensal Species Depend on the Burrow Microhabitat to Complete Their Life Cycle

Changes in plant communities usually cascade to animal communities, such as invertebrates that rely strictly on certain environmental conditions to complete their life cycle. For example, the decline of open, such as semi-natural grasslands and heathlands in Europe, has caused a general decline in biodiversity, especially for butterflies [77]. The digging activity could be effective in reducing grass encroachment and restoring pioneer microhabitats. These usually generate warm, open and sparsely vegetated microsites [78,79]. The low grass cover increased occupancy of the favoured host plant *Pyrgus malvae* indirectly supports effective microhabitat selection by females during oviposition, which strongly determines larval survival. In addition, the importance of mounds created by the European mole (*Talpa europaea*) as an oviposition habitat for the small copper (*Lycaena phlaeas*) within Central European mesotrophic grasslands was reported [80]. The author found that even though *L. phlaeas* is considered a generalist species inhabiting a wide range of open habitats, a high proportion of eggs was found on molehills where the vegetation structure clearly differed from the surrounding vegetation. The oviposition sites of the small copper were preferentially located at open vegetation structures with a higher proportion of bare ground, a lower cover of herbs and a less dense and low-growing vegetation created by the European mole.

Within mesotrophic grasslands, where bare ground is usually rare, mound-building ecosystem engineers act as important substitutes for missing soil disturbance by diversifying the vegetation structure [81] and creating small patches of bare soil that are used for oviposition. Several studies have highlighted the importance of small-scale soil disturbances for the conservation of rare and endangered species [82,83,84,85].

2.4.2 Burrows Providing Shelter and Thermal Refugia for Commensal Animals

Burrowing species are often considered to be important ecosystem engineers, as burrow constructions increase environmental heterogeneity [57,86] and provide shelter and thermal refuge for themselves or other species [5,7,87]. Animals can hide in burrows from fire [88], heavy rain, predators or extreme thermal conditions. Pangolins usually locate their dwelling burrows in secluded places near the top of mountains. The winding passageway of the burrow ensures that the nest room in the burrow will not be flooded in the event of heavy rain [89,90]. In Taiwan, Sun et al. (2018) found that when pangolins stay inside a burrow, the hole is usually blocked with mud, leaving only a small gap at the top of the wall to allow air to circulate [91]. The researchers speculate that this is a way for pangolins to protect themselves from predators, such as the reticulated python (*Python reticulatus*), which preys on Sunda pangolin (*Manis javanica*) [92], while they are inside

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the burrow. Other animals also use pangolin burrows as temporary shelters because of their invisibility and safety. To date, we have monitored more than 37 vertebrates as burrow commensals of the Chinese pangolin; the most frequent users are small mices (unpublished data).

Burrowing engineers can create microhabitats with a more stable temperature and humidity compared to ambient conditions. Gopher tortoises (*Gopherus polyphemus*) are ecosystem engineers that excavate large, deep burrows throughout the coastal plain of the southeastern US [27]. Pike and Mitchell (2013) recorded tortoise body temperatures, operative environmental temperatures (operative environmental temperatures are the temperatures available to an ectotherm in thermal equilibrium with its environment) and burrow temperatures and found that the temperature fluctuations inside burrows were minimal [93]. Bao et al (2013) reported that the air temperature inside the Chinese pangolin burrow was stable, with only a slight fluctuation; in contrast, the air temperature outside the burrow fluctuated dramatically [89].

Recent studies suggest that rising ambient temperatures associated with the overall trend of global warming may make it more difficult for ectotherms to avoid overheating, especially in tropical dry environments [94,95,96]. According to figures from 1981 to 1990, the global average temperature was 0.48 ℃ higher than the temperature 100 years ago. From the beginning of the 20th century to the present, the average temperature of the Earth's surface has increased by approximately 1.1 F (0.6 ℃), and since 2000, the high temperature record has often been broken throughout the world. To avoid extreme (which can lead to death of ectotherms) environmental temperatures and maintain body temperatures within favorable ranges, animals usually changing their diurnal rhythm or search for thermal refuge [97,98]. For example, Walde et al once reported horned larks (*Eremophila alpestris*) using burrows constructed by desert tortoise (*Gopherus agassizii*) in the Mojave Desert during summer as a refuge from the hot above-ground temperatures [79]. Consequently, the function of burrowing engineers that dig burrows and provide thermal refuge for other species is receiving increasing attention from researchers, especially in dry tropical regions where seasonal and diurnal temperatures fluctuate greatly.

2.4.3 Burrows Providing Food Resources for Commensal Species

One important ecosystem function of burrowing engineers is they can alter the distribution of food resources in the environment [1,2,99], furtherly influence the distribution and diversity of species [100,101]. First, bioturbation increasing soil fertility, aggregating seeds and raising the seeds germination, directly increasing plant productivity in the burrow microhabitat [101]. More plant biomass means burrows afford more food resources and attract herbivorous and omnivorous fauna. Additionally, among the species attracted by plant food and thermal refuge, invertebrates account for a huge proportion of the diverse and numerous species, usually regarded as common inhabitants of mammal burrows [6,8,102]. For example, Kinlaw documented 302 invertebrate species in the burrows of gopher tortoise [7]. Hancox documented 81 insect species, including eight tick species, in badger (*Meles meles*) burrows [103], and over 250 invertebrate species were documented to use gerbil (*Gerbillinae*) burrows [6]. Invertebrates are also as food resource provided to other commensal creatures, such as birds, reptiles and amphibians. Galvez-Bravo et al reported that the most common vertebrate taxonomic groups that using rabbit burrows are reptiles and amphibians [104]. The similar viewpoint had been suggested in the study of the prairie dog (*Cynomys ludovicianus*) [105] and pocket gopher (*Thomomys spp*) [106].

Finally, small mices and birds are frequent burrow users, where they forage for seeds or invertebrates. The frequent appearance of these predators also makes burrows become another feeding grounds for more advanced predators, such as medium and large carnivores [7,8,107]. However, these advanced predators may make relatively little use of the burrow, and the burrow is only a spot where they have more prey in their range (personal observation). Most advanced predators have not been monitored using burrows over a long period of time. They enter burrow, search, and leave burrows [108].

2.5 Interaction of Burrow Commensal Species

2.5.1 Burrow Commensal Species Composition and Investigation Methods

Burrow commensal species are animals which was attracted to burrow microhabitats to use burrow resources, and with burrows as the hub, these species form a close bond with each other [5,8,73,102,109,110]. The diversity and richness of burrow commensal animals vary with diggers, investigation methods and monitoring time. The investigation methods vary with animal body size and purpose. Camera traps have been used to monitor medium and large mammals and birds, and it's becoming more common. The methods of monitoring small mammals include live trapping, surveying for signs, tracking, and direct observation; the presence of reptiles and amphibians in burrows is determined by active searches, and they are usually detected at a higher rate in such studies [102,110].

For example, more than 350 species have been documented using gopher tortoise (*Gopherus polyphemus*) burrow systems, of which more than 50 species are vertebrates, including 9 species of amphibians and 25 species of reptiles. The investigation methods included questionnaires, biological traps, and direct observation, the investigation period more than a decade [102]. 57 species have been documented using giant armadillo burrows; 24 species were considered to use either the sand mound or the burrow itself, and 2 reptile species (Tegu *Tupinambis teguixin* and lizard *Ameiva sp.*) were identified. No amphibians have been identified. In this study, camera trap is the only investigation method, the investigation period between July 2010 and September 2012 [5].

Amphibians, reptiles and invertebrates are poikilotherms, and their ability to regulate body temperature is much lower than that of endotherms. It is a biological instinct to use the appropriate environment to assist thermoregulation. We speculate that poikilotherms need thermal refuges as much as birds and mammals, especially in arid and semiarid lands. One reason for the low proportion of amphibians and reptiles in animal monitoring is the over-reliance on camera traps. These cameras are more sensitive to the presence of warmer mammals and birds but less sensitive to the presence of cooler amphibians and reptiles. Another reason may be the short monitoring time and small monitoring area.

2.5.2 Preliminary Study of Burrow Commensal Species Interaction of Chinese Pangolin

Since the survey in 2020, 37 burrow commensal species of Chinese pangolin have been recorded (Figure 5).

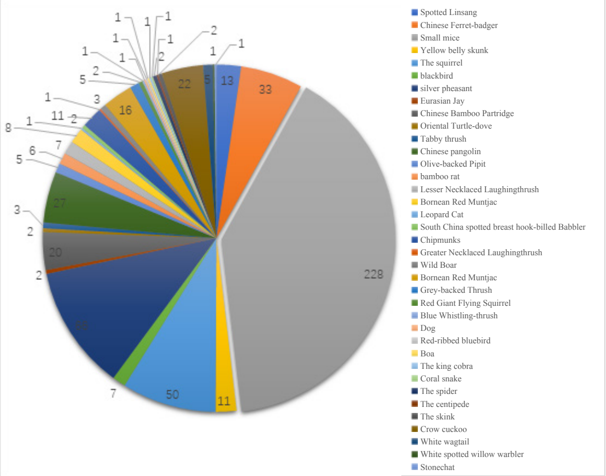

Figure 5. The frequency distribution diagram of Chinese pangolin burrow commensal species.

A total of 14 species of mammals, 17 species of birds, 4 species of reptiles and 2 species of invertebrates were recorded in pangolin burrows. These animals enter the pangolin burrow area directly or forage, mate, comb feathers, etc. Among them, small mices were the most used species in the burrow, with a total of 228 small mice are recorded, accounting for 40%. Followed by silver pheasant (*Lophura nycthemera*; 66), The squirrel (*Sciuridae*; 50) and Chinese Ferret-badger (*Melogale moschata*; 33). Reptiles and invertebrates are less well documented, probably because they are generally smaller and have lower body temperatures than thermostatic species, making them difficult to capture effectively with infrared cameras. Therefore, the utilization rate of ectotherms in the burrow may have been underestimated. At present, an image motion trigger camera has been used to make up for the deficiency.

Pangolin burrows are hot spots of animal activity in the ecosystem. The abundance of burrow resources drives the utilization of burrow commensal species, and complex interspecies interactions are formed during the utilization process. As shown in Figure 5, Chinese pangolin, boa (*Python bivittatus*), spotted linsang (*Prionodon pardicolor*), leopard cat (*Prionailurus bengalensis*), and small mices are the central species in the community of burrow commensal species. Among them, pangolin provides burrow resources for the species, is the basis for the formation of commensal communities, but there is still a risk of being predation by boas and dogs. Boas, spotted linsang, Chinese ferret-badger and leopard cat (*Prionailurus bengalensis*) are predators, which control the biomass of the ecosystem through the top-down effect. Predation is the most frequent interspecific interaction among commensal community, followed by competition with other carnivores. As the most frequent burrow users, small mices themselves also become the indirect burrow resources contributor, attracting other predators. Together with other low-trophic species, they affect community structure through bottom-up effect. The competitive relationship mainly exists among species of the same trophic level (or similar species), which have a high degree of niche overlap and similar demands for habitat, food and other resources.

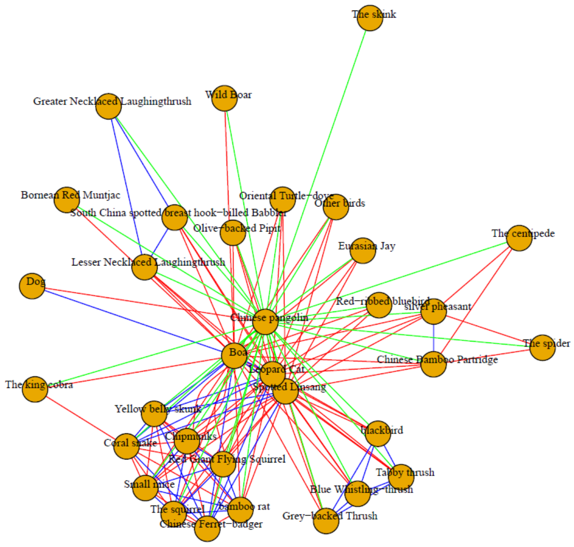

Figure 6. The Chinese pangolin burrow commensal animal population network diagram.

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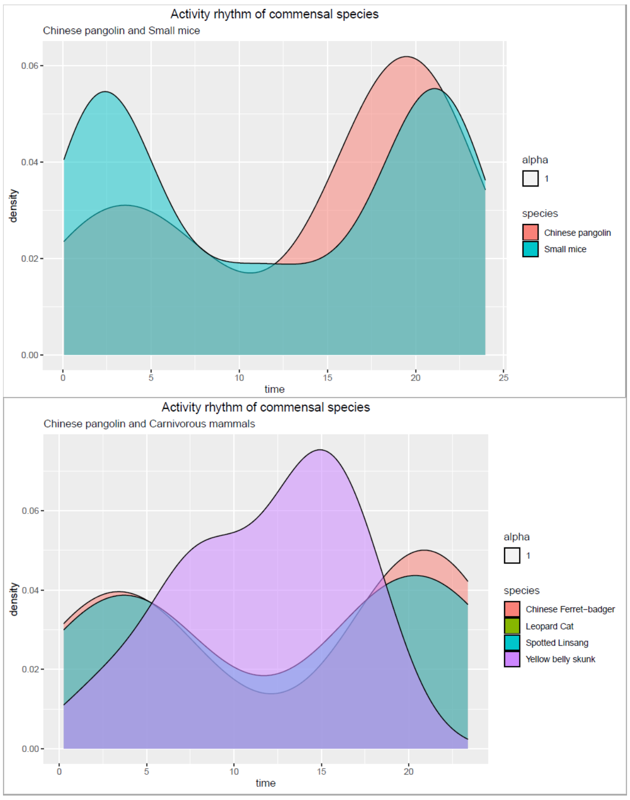
Figure note 1: the green line said there is a commensal relationship between two species (pangolin provide burrow resources) red line said two species predator-prey relationships between the blue line shows the competitive relationship between the two species.

Figure note 2: other birds are crow cuckoo (*Centropus sinensis*), white wagtail (*Motacilla alba*), white spotted willow warbler (*Phylloscopus davisoni*) and stonechat (*Saxicola torquata*).

The activity rhythm map of burrow commensal species showed that the activity peaks of pangolin, small mice, spotted linsang, Chinese ferret badger and leopard cat had a high degree of overlap, and concentrated at night. Yellow belly skunk using their burrows mostly in the daytime, which is inconsistent with their biological habits. The specific reasons need to be further studied. The activity peaks of Phasianidae, Timaliidae and Muscicapidae were basically staggering, which indicated the differentiation of ecological niche to some extent. The activity peaks of carnivorous mammals and small mice basically coincide, and small mice are the common prey targets of the four carnivorous species, which may reflect the rule that low-trophic species influence high-trophic species through bottom-up effect.



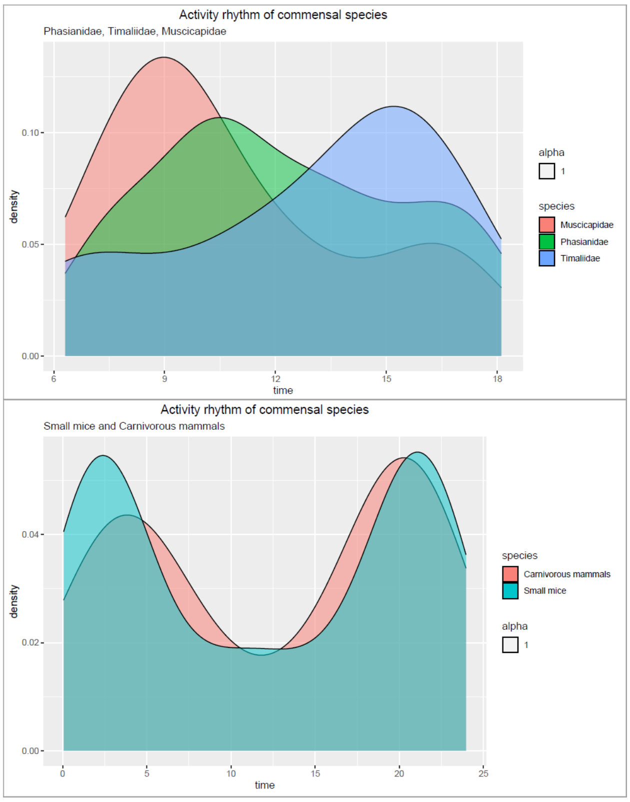


Figure 7. The activity rhythm of Chinese pangolin burrow commensal community

2.5.3 Necessity of Ecological Research on Chinese Pangolins

The Chinese pangolin, once widely distributed in East Asia, northern Southeast Asia, and parts of South Asia, has a range that exceeds three million square kilometres [111]. They once occupied a large area in the south of the Yangtze River in China, but it is hardly to encounter them in most parts of this range in the last three decades. Chinese pangolins are best known for their trophic role as termite predators. Termite is one of the five major insect pests worldwide and damages a variety of trees, water conservancies, and built dams. According to a previous report, 3 kg of pangolin can eat approximately 300~400 g of termites and can protect 17 hectares of forest from termite damage [112]. Therefore, pangolin serve an important role in controlling the termite population in the natural ecosystem. However, previous studies always neglected the fact that Chinese pangolins are ecosystem engineers with the function of modifying surrounding habitats.

The ecological research on Chinese pangolins is very limited, especially regarding the ecological function of their burrows [89,113,114,115]. There is no qualitative or quantitative knowledge of the ecological role of pangolin burrows in the local ecosystem, so it is far from sufficient to speculate based on the relevant studies of other burrowing engineers. Considering the extensive distribution area and enormous burrows of Chinese pangolins before the 1980s, we think pangolins must be an important regulator of the ecological balance in the ecosystems [111,116,117,118,119,120]. On the one hand, pangolin is a narrow-eating mammal that feeds mainly on termites, and it plays an indispensable role as a termite damage controller in the ecosystem. Furthermore, many species of termites (such as *Coptotermes formosanus*, *Odontotermes formosanus* and *Macrotermes barneyi*) live in nest, with their nests changing topography and landforms and altering the distribution of resources in the environment. These species are also to be ecosystem engineers according to Jones and Lawton's proposed definition [1,2]. That is, their predation behavior affects the ability of another kind of engineer to transform the ecosystem. On the other hand, burrows provide shelter, thermal refuge and food resources for burrow commensal species, the negative impact on the survival of commensal species of pangolins, which have declined dramatically in recent decades and even become extinct regionwide, is still unknown. Several studies have shown the decline in biomass, species richness, and abundance of vertebrate species in areas where burrowing engineers have been eradicated [121,122,123]. For instance, the extinction of prairie dogs has caused the near-extinction of black-footed ferrets (*Mustela nigripes*) and the drastic decline of mountain plovers (*Charadrius montanus*) [124]. Taking into account pangolins' ability to physically modify their habitats, their profound impact on commensal species, and their unique position in the food web, we conclude that pangolins play a key role in their ecosystem. Therefore, it is necessary that continuous study of pangolin ecology for a long time.

3. Negative Feedback of Engineering Effects on the Ecosystem

Not all the physical modification made by burrowing engineers to the habitat are positive, some studies have mentioned the negative effect for the habitat caused by the digging behavior of organisms. However, there has been relatively little research on the negative effects of burrowing engineering, so we are here to briefly discuss them. Firstly, excessive digging activity tends to destroy the ground surface, increase bare land area, and accelerate surface erosion [12,125,126,127]. Overdigging is often associated with a high-density population of engineers. From this point of view, the effect of engineers' digging activity on the ecosystem can't be purely qualitative. Moderate excavation is beneficial to soil renewal, while excessive excavation is destructive, which is also in line with the ecological hypothesis that moderate disturbance increases biodiversity. Therefore, it is very necessary to study at population scale and landscape scale. In addition, the bare ground will reduce vegetation cover [125,128,129,130] and lead to the invasion of alien species [131]. And the change of soil physicochemical properties will also inhibit the colonization of some species [132]. The negative feedback of engineering effects on ecosystems can also be seen in animal communities, for example, the digging behavior of cape ground squirrels (*Xerus inauris*) changed vegetation community structure and further decreased habitat quality of beetle, this ultimately leads to a decline in beetle richness [43].

4. Suggestions for Future Direction and the Way Forward

The loss of biodiversity is currently one of the most important issues in the world. In this review, we briefly list some positive effects of burrowing engineers on biodiversity, such as increasing geomorphological heterogeneity, promoting plant community renewal and providing resources for many groups [7,63]. The ecological impact of these burrowing engineers is more intense in environments otherwise unfavourable for most species considered [104]. Indirect conservation by protecting an important species and using its irreplaceable ecological role to benefit other organisms is a much easier and more practical approach than aimless extensive conservation. Consequently, management actions to preserve endangered burrowing engineer populations worldwide are necessary to maintain their effects on vegetation and animal communities.

To better use burrowing engineer species for habitat remoulding functions in ecosystems and equip us for the future challenges of ecological and conservation science, more detailed research is needed on:

(1) Burrowing engineer ecological cascades through trophic and engineering pathways and their mixed effects on ecosystems.

(2) Categorizing burrowing engineers according to the action and scope of their engineering effects (e.g., comprehensive assessment of impact duration, the number of species affected, body size, population density, etc.).

(3) The spatiotemporal relationships of burrow commensal species and the driving mechanisms.

(4) Emerging studies of engineer reduction and reintroduction.

(5) The entire periodic effects of burrows on soil,

vegetation, and commensal species (i.e., the process from bioturbation being started to burrows being assimilated into the environment).

5. Conclusions

We summarized the habitat modification function of burrowing engineers from five directions, emphasized the critical role that the rejuvenation of engineer species can play in mitigating the ongoing loss of biodiversity. It's providing a strong theoretical support for the necessity of the protection work of burrowing engineers. We also summarized the experimental design methods of burrowing engineer studies, the dominating experiment method is comparative measurement. Researchers are comparing soil properties, plant community structure between disturbed and undisturbed areas at different spatial and temporal scales. This research method is easy to reveal part of the ecological role of burrowing engineers, but it is not conducive to explore the deeper potential impact of engineers on the habitat. More diversified experimental design (e.g. manipulative experiments, replication across multiple sites) and more scientific and accurate data analysis (e.g. mathematical model) are necessary. At present, the most urgent task is to apply the theory of ecosystem engineer to the work of biological protection, and bring into play the ecological role of burrowing engineer in modificating the habitat and regulating the community structure of commensal species. Long term research of engineering impact on ecosystem at population scale is essential, the research on the ecological role of burrowing engineers in humid and subhumid areas also needs to be strengthened. This article aims to identify some implications to better understand the interaction between the burrowing engineer and local habitat. It is our sincere hope that this review will contribute to the conservation of the Chinese pangolin and many other burrowing engineer species.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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