World Journal of Microbiology and Biotechnology (2022) 38: 213
https://doi.org/10.1007/s11274-022-03373-7

RESEARCH

Autochthonous nutrient recycling driven by soil microbiota could be sustaining high coconut productivity in Lakshadweep Islands sans external fertilizer application

Murali Gopal[1,4] · Alka Gupta[1] · V. Arunachalam[1,2,4] · H. P. Maheswarappa[1,3] · George V. Thomas[1,5] · P. M. Jacob[4,6]

Received: 23 March 2022 / Accepted: 29 July 2022 / Published online: 2 September 2022

Abstract

The soils of Lakshadweep Islands are formed as a result of the fragmentation of coral limestone, that is carbonate-rich, with neutral pH, but poor in plant nutrients. Coconut palm (*Cocos nucifera* L.) is the main crop cultivated, supporting the life and livelihood of the islanders. No external fertilizer application or major plant protection measures are adopted for their cultivation as the Islands were declared to go organic decades back. Yet, Lakshadweep has one of the highest productivity of coconut compared with other coconut growing areas in India. Therefore, a question arises: how is such a high coconut productivity sustained? We try to answer by estimating in three main islands (i) the nutrients added to the soil via the litter generated by coconut palms and (ii) the role of soil microbiota, including arbuscular mycorrhizae, for the high productivity. Our results indicated that, besides adding a substantial quantum of organic carbon, twice the needed amount of nitrogen, extra 20% phosphorus to the already P-rich soils, 43–45% of potassium required by palms could be easily met by the total coconut biomass residues returned to the soil. Principal Component Analysis showed that soil organic carbon %, potassium, and organic carbon added via the palm litter and AM spore load scored $> \pm 0.95$ in PC1, whereas, available K in the soil, bacteria, actinomycetes, phosphate solubilizers and fluorescent pseudomonads scored above $> \pm 0.95$ in PC2. Based on our analysis, we suggest that the autochthonous nutrients added via the coconut biomass residues, recycled by the soil microbial communities, could be one of the main reasons for sustaining a high productivity of the coconut palms in Lakshadweep Islands, in the absence of any external fertilizer application, mimicking a semi-closed-loop forest ecosystem.

Keywords Lakshadweep Islands · Coral soils · Coconut palm litter · Soil microbiota · Arbuscular mycorrhizae · Nutrient recycling

Introduction

Lakshadweep is a tropical archipelago consisting of 36 islands located near the south-western coast of India alongside the state of Kerala. The islands are surrounded by the Laccadive Sea and dominated by narrow and specific terrestrial-ecological conditions viz. lagoon and reef-fringed ecosystems rich in marine fauna, shallow and nutrient poor soils of coral lime-stone origin (Krishnan et al. 2004) supporting a limited flora of trees and shrubs with coconut being the predominant crop, a high water table recharged only by the southwestern monsoon juxtaposed with long dry periods; temperatures ranging between 25 and 35 °C and a relative humidity of 70–76%. Out of the 36 Islands, 11 of them, viz. Androth, Kalpeni, Kavaratti and Minicoy contribute to maximum area under coconut followed by Amini, Bitra, Agatti, Chetlat, Kiltan, Kadamat and Suheli

✉ Murali Gopal
mgcpcri@yahoo.co.in

✉ Alka Gupta
agcpcri@yahoo.co.in

[1] ICAR-Central Plantation Crops Research Institute, Kasaragod, Kerala, India

[2] ICAR-Central Coastal Agricultural Research Institute, Ela, Goa, India

[3] University of Horticultural Sciences, Bagalkot, Karnataka, India

[4] ICAR-Central Plantation Crops Research Institute, Regional Station (Presently ICAR-CIARI), Minicoy, Lakshadweep, India

[5] Present Address: Pathanamthitta, Kerala, India

[6] Present Address: Kottayam, Kerala, India

Valiyakara. Overall, with 2570 ha of the total 3228 ha of Lakshadweep land mass of the islands under coconut palms (Thamban et al. 2020), it forms the agricultural mainstay of the inhabitants in terms of their economy along with tuna fishing, its processing and export. Coconut palms grown in Lakshadweep islands display high productivity, and desirable traits of high oil content and drought tolerance. The main coconut varieties cultivated are Laccadive Ordinary Tall (LCT), Laccadive Micro Tall (LMT), Kaithathali Tall, and Laccadive Orange Dwarf (Jacob and Krishnamoorthy 1981). Remarkably, without the addition of any substantial amount of fertilizers and grown at a highly dense rate of > 400 palms like a forest (Gopal 2000) instead of the recommended 175–200 palms per ha, the coconut productivity of Lakshadweep islands currently at 30,623 nuts/ha remains the highest in India (Thamban et al. 2020). Per palm yield easily ranges between 70 to 100 nuts annually (Shameena Beegum et al. 2022). Not only productivity, the oil content of the Laccadive Ordinary Tall and Laccadive Micro Tall, on an average, is about 74% (Patil et al., 1993; Ratnambal et al. 1995); a good 5–8% more than tall varieties cultivated in mainland areas of southern India. The palms are also known to have resistance to water stress, and therefore have been used as female parent material for developing drought-tolerant hybrids viz Lakshaganga and Chandralaksha (Rajagopal et al. 1990).

With reducing arable land availability, increasing soil erosion (Mandal and Tripathi 2009) that depletes the plant nutrients and nil external fertilizer application, such a high nut yield, and productivity, coupled with high oil yield, could be sustained only if there is a regular supply of essential nutrients made available to the palms. Application of inorganic fertilizer, which could seriously contaminate the limited groundwater source, was completely banned in Lakshadweep Islands from the year 2000 owing to their precarious ecological conditions. Subsequently, adding fertilizers was promoted for agricultural purposes, particularly for raising fruits and vegetables but not for the coconut palms. Coconut palms, thus, by and large, are grown without any fertilizer application. Under these crop production circumstances, it is rather confounding that the coconut yield and productivity is sustained at a national high in Lakshadweep Islands, particularly in the absence of external fertilizer application.

One of the possible clues in support of the high productivity factor in coconut is the excellent organic matter content and near neutral pH recorded in the soils of Lakshadweep. The presence of organic matter adds important plant nutrients, post mineralization by soil microbiota, to the soils, which become easily available at the neutral pH. The high organic matter in soil may not be significantly contributed by the allochthonous nutrient sources such as the seaweeds and fish debris, rich in proteins and amino acids, that accumulate along the shores of the Islands. Though bird guano is another source of nutrients, this is drastically reduced because of coconut cultivation, increasing population and settlement area that have deterred the sea birds from nesting in the Islands (Pande et al., 2007; Young et al. 2009).

The other possible nutrient sources to the coconut palms in the Islands could be rainfall or plant litter. Precipitations brought in by monsoon deposit about 38.0 kg^{-1} ha^{-1} of NO_3^- and 15.6 kg^{-1} ha^{-1} of SO_4^{2-}annually in Minicoy and cations such as Na, Cl, Mg and K (Soni 2021). Similar quantities could be getting deposited by precipitation in the other islands of Lakshadweep too. Sea water sprays aid in sodium, potassium and chlorine uptake. However, they are insufficient to fertilize the coconut palms particularly when its NPK requirement is to the tune of 500 g N, 320 g P_2O_5 and 1200 g K_2O/palm/year along with application of organic manure @50 kg/palm or 30 kg green manure for good productivity (Nelliat 1973). Litter fall from above ground vegetation has been reported as an important source of nutrients in islands (Smith et al. 2008; Batianoff et al. 2010), and leaching from such litter releases phosphate which functions as an autochthonous nutrient source in peat swamps (Ong et al., 2017).

This study attempts to answer the question of high productivity and desirable traits of coconut palms in Lakshadweep islands despite grown on nutrient poor soils, not applied with any external fertilizer, at high inter plant competition by high plant density.

Under this scenario, we hypothesized that the possible reasons for the sustained high coconut productivity in the poor coral soils of Lakshadweep, encountering narrow and specific terrestrial-ecological spectrum, could possibly be driven by recycling of nutrients added by palm litter and plant-beneficial microbiota in the near-forest kind of coconut ecosystem. This hypothesis reflects the studies that have proved that bulk of the nutrients required for plant growth in Island conditions is obtained by the decomposition of plant litter and peat as reported in Marion islands (Smith et al. 2008). Therefore, to ascertain this hypothesis, we analyzed autochthonous nutrient availability via crop litter and the rhizosphere microbiota and arbuscular mycorrhizae (AM) association in coconut palms cultivated in three important Islands of Lakshadweep: Kavaratti, Kalpeni and Minicoy, and present the findings in this paper.

Materials and methods

Autochthonous nutrient estimation

The autochthonous nutrient pool available within the island was estimated by computing the NPK returned to the soil via the litter addition from the vegetation growing in the Islands. Coconuts being the predominant vegetation covering almost the entire islands, the data on the area (ha) under coconut, the total number of palms growing and the average coconut yield year^{-1} (lakh nuts) in the three Islands were collected from the Agriculture Department, Union Territory of Lakshadweep and were used for calculating the nutrients added to the soil from their biomass residues such as leaf fronds and husks (Suppl. Figure 1). It is well established that about 8 tonnes leaf fronds from one-hectare coconut garden and close to 35% of husk from each coconut is generated as residues (Biddappa et al. 1996). The nutrient values in the leaf and coconut husks of Lakshadweep Islands (Singh and Velayutham 1979) were used to estimate the total N, P, and K available from these sources to the soil. The allochthonous nutrient sources such as bird guano, fish wastes (from tuna processing units and households' food wastes), and seaweed accumulation to the tune of 10,000 to 19,000 tonnes (wet biomass) along the 12 atoll coasts (Kalidharan 2001) need more thorough analysis to be accounted as a significant source of nutrients for coconut.

Vegetation survey and soil sample collection

Three important Islands of Lakshadweep viz. Kavaratti (the capital), Minicoy and Kalpeni were selected for the study and collection of vegetation data and soil samples. A transect walk was carried out across the length and breadth of the Islands and the vegetation found growing in a 15 × 15 m plot were listed from the following categories (i) coastal stretch (shore), (ii) stretch between the coasts and mid island (inshore) (iii) middle and hinterland (inland) area of the island. The sampling was carried out based on the length, breadth and accessibility to shores of the Islands. Soil sample collection was carried out twice. In the first study, Minicoy and Kalpeni were included. Adopting standard protocol, soil samples were collected from the top 30 cm depth after clearing any plant/organic matter debris in the same 15 × 15 m plots characterized for the vegetation in the transect walk. A minimum of three 15 × 15 m plots for three categories were used. From each 15 × 15 m plot, five soil samples were collected, homogenized and bagged. In the second sampling, Minicoy, Kalpeni and Kavaratti were included and only rhizosphere soil with small freshly growing active roots were collected from high yielding coconut palms. An auger was used for the collection of the samples from three different spots from the basin (one metre area around the bole of the palm) of each palm at the 0–30 cm depth. The three sub-samples were pooled together to represent a sample from one palm. A minimum of six palms were sampled during this soil sampling. Soils were transferred to clean polythene bags, transported to ICAR-CPCRI in cold conditions (4 °C) and then stored in refrigerator for the microbial analysis. One set of samples were air-dried and passed through a 2 mm sieve, mixed thoroughly to obtain composite sample, and used for soil physical and chemical analysis.

Soil physico-chemical analysis

The pH of the soil was measured in 1:2.5 soil-water suspension using a pH meter (Eutech Instruments). The soil organic carbon was analyzed following Walkley and Black (1934) rapid titration method. The primary, secondary, and micronutrients were also estimated. Total nitrogen was analyzed by Kjeldahl digestion and steam distillation (Jackson 1973) while the available phosphorus was determined using the method of Olsen et al. (1954). Available potassium was estimated by ammonium acetate extraction (Hanway and Heidel 1952) using flame photometer (Systronics Flame Photometer 128). Secondary (Ca and Mg) and micronutrients (Fe, Mn, Cu and Zn) were estimated using an Atomic Absorption Spectrophotometer (Varian SpectrAA 55) adopting the procedure of Lindsay and Norvell (1978).

Soil microbial analysis

General and function-specific microbial communities

The first set of soil samples collected from transect walk plots were estimated for the general microbial communities such as bacteria, actinomycetes and fungi and function-specific microbiota viz. cellulose degraders, free-living nitrogen fixers, nitrifying bacteria (nitrifiers and nitratifiers) and phosphate solubilizers adopting serial dilution and pour plate culture-dependent method. The nitrifying bacteria were estimated using the most probable number (MPN) method, while all others were through serial dilution and plating method on specific selective medium, as described in our previous work on soil microbial analysis of monocropped coconut palms applied with systemic soil insecticide and neem cake (Gopal et al.2001). Clear zone formation by cellulose-degrading microbiota was enumerated after flooding carboxymethyl cellulose agar plates with Gram's iodine solution (Kasana et al.2008).

Arbuscular mycorrhizae

The second set of soil samples collected from the coconut rhizosphere were analyzed for arbuscular mycorrhizae (AM) spore population and root association in addition to the general and function-specific microbial communities. For estimating the AM colonization, fresh, cream-coloured roots were selected from each sample, cut into 1 cm segments using a fine blade and fixed in formalin: aceto: alcohol solution (90:5:5). Following the process described by Phillips and Hayman (1970), the fixed roots were then processed by washing with two changes of tap water, transferred into a boiling tube containing 10% KOH and autoclaved at 121 °C for 3 min for the clearing of the roots. After autoclaving, the KOH solution was poured off and the root bits were washed in three changes of tap water. Further, the roots were bleached using alkaline H_2O_2 for 10 min at room temperature. Then, the roots were washed thoroughly with water and immersed in 1% HCl for 10 min. The acid was then decanted off and the roots were stained in 0.05% trypan blue in lacto-glycerol and boiled for 20 min at 90 °C. Destaining was done using lacto glycerol solution and the roots were observed under the microscope (Leica) for AM colonization by scoring the presence of vesicles, arbuscules and hyphae.

In order to quantify the colonization, ten numbers of one cm root bits were placed in clean glass slide and observed under high magnification for the presence of vesicles, arbuscules and hyphae. Percentage of root colonization by AM was calculated using the formula –

$$\%\ \text{Root colonization} = \frac{\text{Number of root bits having colonization}}{\text{Number of root bits observed}} \times 100$$

AM spore population estimation

AM fungal spores were extracted by wet sieving (45, 100, 250, and 355 μm sieve openings) and decanting method (Gerdemann and Nicholson 1963). The spores extracted through sieves, with mesh sizes ranging between 45 and 355 μm, were filtered using a Whatman No.1 filter paper and were observed under a stereo microscope, and the total number of spores was counted. Spores exhibiting morphologically similar characters were then clustered into one group. To derive spore community composition, the number of spores in each morphotype was recorded. Spore count was calculated as the total number of spores in each soil sample (spores per 10 g soil).

Statistical analysis

Standard deviation was calculated for most of the data. Further, the variations in the AM fungal population and number of species between different Islands were tested statistically along with microbial populations by Duncan's Multiple Range Test (DMRT). Pearson's correlation coefficient was calculated between soil chemical and mycorrhizal parameters. Simpson's diversity index and Shannon's diversity index were calculated for the microbial population count data following Simpson (1949) and Lloyd and co workers (1968), respectively. Altogether, a Principal Component Analysis of 17 variables of Islands including soil nutrient values, nutrients returned via residues, microbial population, etc. was performed using varimax rotation method by SPSS package.

Results

Autochthonous nutrient addition

The area under coconut in each of the three Islands was used to compute the nutrients returned to the soil from coconut fronds and husks. Area-wise, Minicoy had the largest holding (426.1 ha) followed by Kavaratti (392.4 ha); however, number of palms were more in latter (164,808) than the former (146,962). The palm density was thus higher in Kavaratti among the three Islands. The nitrogen (N), phosphorus (P), potassium (K) and organic carbon (OC) added by the biomass residues from coconut palms (Fig. 1), that covered more than 85% of the vegetation area, was estimated. The results showed that nitrogen and potassium recycled annually was highest in Kavaratti (67.5 tonnes N, 45.8 tonnes K), followed by Minicoy (66.3 tonnes N and 38.4 tonnes K). The phosphorus returned ranged between 3.2 and 5.1 tonnes in the Islands. Organic carbon addition also followed the same pattern; Kavaratti with maximum of 1737.57 tonnes and Minicoy with 1458.03 tonnes, annually (Table 1).

Vegetation diversity

Transect walk to capture the vegetation of the three Islands gave similar scenario, with coconut palm (*Cocos nucifera* L.) being ecologically the dominant one covering almost 80–90% of the area. Along the coastal stretch, much of the area was free of vegetation. However, in some places *Scaevola koenigii* (locally called Kanni), *Pandanus odoratissimus* (screw pine, locally called Kaitha), *Pemphis acidula* (locally called cheruthalam), *Casuarina equisetifolia* (casuarinas), *Morinda citrifolia* (noni), *Spinifex littoreus* and *Tournefortia argentea* (Tamara) were commonly recorded. In addition to these, patches of sea grass such as *Thalassia hemprichii* and *Cymodocea isoetifolia* were also observed. The next 100 to 200 m range from the shore (inshore) was mostly populated with *Cocos nucifera* (coconut palm) interspersed with *Musa paradisiaca* (banana), *Artocarpus incise* (breadfruit), *Terminalia catappa* (wild almond), *Moringa oleifera* (drumstick), *Agave americana* (agave), *Morinda citrifolia* (noni) and *Zizyphus zuzuba* (jujube, *elanthapazham* in local language). The third area, inland, including some low lying areas in the Islands, was again dominant with coconut, banana, *Pandanus odoratissimus*, agave and shrub vegetation. In the settlement

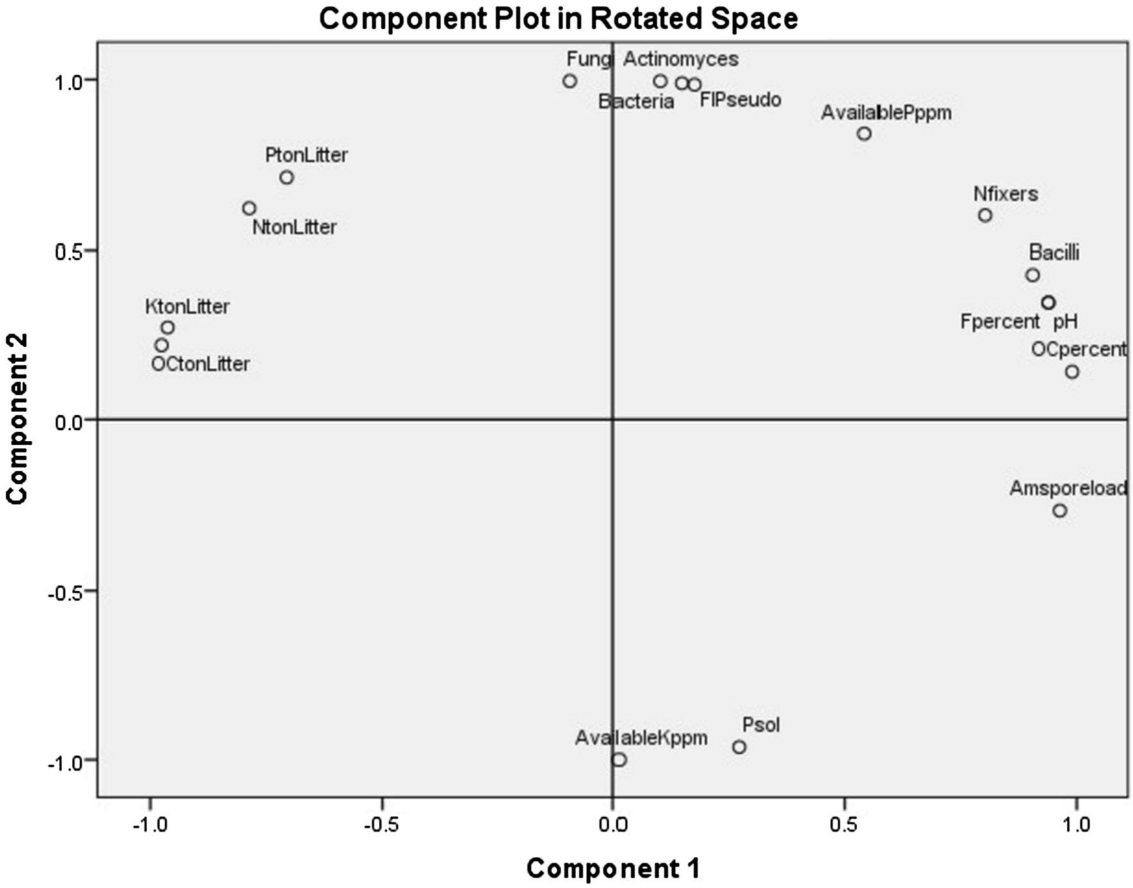

Fig. 1 Component plot in rotated space for the 17 variables analyzed by PCA for the three Lakshadweep Islands indicating key factors influencing the high coconut yield. The soil organic carbon %, potassium, and organic carbon added via the palm litter and AM spore load scoring > ± 0.95 in PC1, whereas, available K in the soil, bacteria and actinomycetes, phosphate solubilizers and fluorescent pseudomonads scored above > ± 0.95 in PC2

area, vegetables like tomato, chilli, okra and others, tubers such as taro, betel leaf (*Piper betle*), papaya were grown by the inhabitants.

Soil fertility status

The physico-chemical properties of the Islands' carbonatic soils were analyzed twice, with the first analysis being elaborate for two Islands at three different sites (shore, inshore and inland) (Suppl. Table 1). The pH of the soils in the three sites (shore, inshore and inland) of two Islands as well as the coconut rhizosphere from three Islands were close to neutral to slightly alkaline (pH 6.6 to 7.5). It could be noticed that the organic carbon (OC) ranging from 0.12 to 3.1% and zinc (Zn) contents of 2.7 to 9.8 ppm increased from the shore to the inland sites. The N, P and K contents did not follow the same increasing trend and ranged between 0.1 and 0.2%, 39 and 56 kg/ha, and 85 and 151 kg/ha, respectively (Table 2). The second analysis focused towards the rhizosphere soils of coconut from three Islands viz., Kavaratti, Kalpeni and Minicoy (Table 2). The pH of the rhizosphere soil of coconut palms in all the three Islands was alkaline ranging closely between 7.5 and 7.6. The OC values were close to 1 and 1.5% with slightly lower available P but higher K availability (Table 2) than general soil sampling data from the first studies.

Soil microbial analysis

In the first set of soils sampled from Kalpeni and Minicoy, population of general (bacteria, actinomycetes and fungi) and plant-beneficial (free living N-fixers, phosphate solubilizers, cellulose degraders and nitrifying bacteria) microbial communities at different spatial points: shore, inshore and inland soils, were enumerated. Among the three general communities studied, populations of bacteria ($0.11–1.02 \times 10^5$ cfu/g dry soil) and actinomycetes ($0.2–6.1 \times 10^4$ cfu/g dry soil) was seen to be more than fungal colonies ($1–7 \times 10^3$ cfu/g dry soil) in both the Islands. Among the function-specific microbiota analyzed,

Table 1 Details of area and total number of coconut palms under cultivation in selected Lakshadweep Islands, annual production of nuts, and biomass residues available from these palms, total quantity of major nutrients locked in the residues and their return to soil

Island	Av. Area (ha)^	Total no. of palms^	Av. Production (lakh^^ nuts)	Husk residues produced* (tonnes)	Major nutrients from husks** (tonnes)			Leaf and other palm litters (tonnes)	Nutrients from leaf and other palm litters *** (tonnes)			Total nutrients returning to soil from the palm residues (tonnes)			Approx. OC from the residues (tonnes)
					N	P	K		N	P	K	N	P	K	
Kavaratti	392.4	164808	139.6	3175.9	13.65	0.51	25.72	3139.2	53.36	4.40	20.10	67.01	4.91	45.82	1815.86
Kalpeni	258.5	108570	89.3	2024.75	8.71	0.32	16.40	2068.0	35.17	2.89	13.23	43.88	3.21	27.74	1159.45
Minicoy	426.1	146962	85.1	1933.7	8.31	0.31	15.66	3408.8	57.95	4.80	22.81	66.26	5.11	38.47	1630.77

^ Obtained from Agriculture Department, Union Territory of Lakshadweep and Thamban et al., (2020) ^^ Ten lakhs equal one million

*Husk residues calculated by taking full coconut weight as 650 g with husk at 35% of the full nut weight (by utilizing the nut characteristics data of Laccadive Ordinary Tall and Laccadive Micro Tall, Ratnambal et al. 1995; Biddappa et al. 1996)

** Nutrient contents from husk calculated by taking NPK values in husk as 0.43, 0.016 and 0.81% respectively, and 30% OC (Dr. Radhakrishnan, Central Coir Research Institute, Alleppey, personal communication)

*** Nutrients from leaves and other wastes calculated by taking: 1.7% N, 0.14% P, 0.64% K (Singh & Velayutham, (1979)

population of free-living nitrogen fixers, cellulose decomposers and nitrifying bacteria were observed to be higher in the inshore and inland sites compared to shore soils of the Islands. However, phosphate-solubilizing bacteria were mostly found in low population (100–200 cfu/g dry soil) and that too in the inshore and inland sites; they could not be detected in the shore soil samples with the adopted methodology (Suppl. Table 2).

Log_{10} transformed values of the general and functional microbial communities of second set of soil samples collected from the rhizosphere of coconut palms of Kavaratti, Kalpeni and Minicoy indicated a higher population of bacteria, fungi and actinomycetes compared to first soil sampling data. A thriving population of bacteria (6.6–7.0), actinomycetes (6–7) and bacilli (above 6) was observed. Among the function-specific microbiota, population of nitrogen fixers was more in Kalpeni Island whereas fluorescent pseudomonads were more in Minicoy (Table 3).

The spore numbers and root association index of the important root-fungi symbiosis, arbuscular mycorrhizae, were also assessed in coconut rhizosphere during the second soil analysis (Table 3). The highest AM colonization was recorded from rhizosphere of coconut from Kalpeni and Minicoy islands (61%) and the lowest in Kavaratti (53%). The arbuscular mycorrhizal fungi identified based on the spore morphology belonged to the genera of *Glomus, Gigaspora, Acaulospora* and *Scutellospora* (Suppl. Figure 2). Simpson's diversity index (Ds) and Shannon's diversity index (Hs) in three different islands of Lakshadweep were analyzed (Suppl. Figure 3). The index value of "Ds" and "Hs" varied from 0.159 to 0.505 and 0.483 to 1.119, respectively. Arbuscular mycorrhizae fungal species' dominance in Kalpeni Island (0.505, 1.119) was slightly higher than that in Minicoy (0.372, 0.929) and Kavaratti (0.159, 0.483).

Principal component analysis

The analysis of 17 variables by PCA showed that PC1 and PC2 contributed 100% of the variability in the data set. The soil organic carbon %, potassium and organic carbon added from the palm litter to the soil and AM spore load scored > ± 0.95 in PC1, whereas available K in the soil, bacteria and actinomycetes in the general microbial community, and phosphate solubilizers and fluorescent pseudomonads among the function-specific microbial communities scored above > ± 0.95 in PC2 (Suppl. Table 1). The plot of PC1 and PC2 rotated component matrix of 17 variables by PCA of the three Lakshadweep Islands is furnished in Fig. 1.

Table 2 Physico-chemical properties of rhizosphere soils of coconut collected from three islands of Lakshadweep (second set of studies)

Name of islands	pH	OC (%)	Available P (Kg/ha)	Available K (Kg/ha)
Kalpeni	7.60 ± 0.04	1.61 ± 0.22	180.04 ± 30	117. 09 ± 16
Kavaratti	7.55 ± 0.05	0.93 ± 0.27	170.92 ± 36	92.42 ± 19
Minicoy	7.60 ± 0.04	1.46 ± 0.22	134.18 ± 30	159.30 ± 16

Table 3 Microbial populations (Log CFU/g dry soil) in the rhizosphere soils of coconut collected from three islands of Lakshadweep (second set of studies)

Location	Bacteria	Fungi	Actinomycetes	P-solubilizers	Fluorescent Pseudomonads	Free-living N-Fixers	Bacilli	F% for AM	AM Spore load/10 g soil
Kalpeni	6.62^{b}	4.58^{a}	6.62^{b}	3.92^{a}	1.29^{b}	2.68^{a}	6.83^{a}	61.11^{a}	81.33^{a}
Kavaratti	6.64^{b}	4.60^{a}	6.68^{b}	3.71^{b}	1.20^{b}	1.31^{a}	6.58^{a}	53.33^{a}	63.66^{b}
Minicoy	7.06^{a}	4.65^{a}	7.08^{a}	3.97^{a}	2.93^{a}	1.79^{a}	6.85^{a}	61.11^{a}	70.55^{ab}

F%—Frequency of AM colonization

Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test

Discussion

Autochthonous nutrients

Being somewhat semi-closed-loop forest-type ecosystem in the Lakshadweep Islands, the residues from the vegetation were considered to be returned to the soil (Suppl. Figure 1). It is well known that litter fall is one of the critical sources of nutrients returned to terrestrial ecosystems, particularly of forest types and leaf tissues were implicated for more than 70% of the litter (Robertson and Paul 1999). Moreover, in the case of coconut, it had been determined that through meticulous recycling of all the usufructs, about 20.7 kg N, 10.5 kg P_2O_5 and 30.8 kg K_2O could be ploughed back in the mainland scenario (Jothimani 1994). Decomposition of coconut husks had also been shown to add key nutrients to the soil, that is known greatly to reduce the inorganic fertilizer requirements (Ouvrier and de Taffin 1985). Lakshadweep islands being heavily populated with coconut palms, the amount of residues in terms of leaves, inflorescence and bunch wastes and coconut husks was of substantial quantum (Table 1). An estimation of the quantities of N, P, K and organic carbon (OC) able to be recycled annually indicated that higher amounts were generated in Kavaratti followed by Minicoy, largely due to the area under coconut and the number of palms growing there. The litter fall would have undergone decomposition and supplied the nutrients to plants and microbial biomass. Thus, several tonnes of N, P, and K were made available to the palms for their growth and productivity in the Lakshadweep Islands. Being from the same source, *i.e.* palm to palm, the nutrient uptake perhaps must had been efficient. The pH of the soil of Lakshadweep was close to neutral (Krishnan et al 2004), which again would have helped in better nutrient mineralization, release and availability to the palms. Solar radiation (photosynthetically active radiation and ultraviolet radiations) is another agent known to promote the decomposition of leaf litter (Barnes et al. 2015). Lakshadweep is known to receive on an average 16 MJm^2 of solar radiation energy, with Minicoy getting higher than 18 MJm^2 (Tyagi 2009), which must also be promoting the litter decomposition to some extent along with the soil-based biological factors.

Based on 2017–18 data available with the Agriculture Department, UT of Lakshadweep, Kavaratti, Minicoy and Kalpeni had approximately 164,808, 146,962 and 108,750 palms, respectively at a density of more than 400 palms per ha (Thamban et al. 2020). The recommended annual dose of N, P and K for adult coconut palm in the mainland was 500 g N: 320 g P_2O_5:1200 g K_2O (Nelliat 1973). The nutrients from recycled residues (Table 1) could meet more than 80% of the N, 10% P and 20% K of this recommended fertilizer dose in the islands. However, per detailed manurial trials conducted in Lakshadweep during 1983, wherein 6 different NPK treatments including control were evaluated, an annual fertilizer dose of 250 g N, 160 g P_2O_5 and 600 g K_2O was recommended for coconut palms growing in Lakshadweep (Bopaiah and Cecil 1993). The recycled residues, therefore, could meet twice the amount of N, add in excess of 20% P to the already phosphate-rich soils, and meet more than 40% of K requirement of the palms as per the manurial recommendation for the Islands (Bopaiah and Cecil 1993). Thus, it was clear that, without any external application of fertilizers, N and P requirements were fully met and the demand for K was met as much as 43–45% by the recycled coconut litters. Even if 50% of the biomass residues was considered to reach the soil, rest 50% being accounted for use as fuel, thatching, making brooms and for other sundry purposes by the islanders, yet full requirement of N and P and above 20% K requirement of coconut palms was met.

Vegetation

The vegetation pattern observed in Minicoy, Kalpeni and Kavaratti was a typical forest type ecosystem seen in tropical and sub-tropical islands, with coconut palms reaching the level of mono dominance in these islands, as reported earlier in other atolls in the Central Pacific (Young et al. 2009). The main livestock present in the islands were the cattle, goat and poultry. We aimed to record the main vegetation growing in the islands and not an exhaustive one. The trees and shrubs that we could identify matched with the earlier reports on flora and fauna of the Lakshadweep islands (Joseph John et al. 2018). The density of the trees and other plants was found to be very high in the islands. Earlier estimates had mean basal area available for plantation as 14.64 m^2, and for littoral vegetation to be $1.41 m^2$, with maximum species diversity observed in the littoral vegetation (IIRS, 2010). High above-ground biomass density per unit area was reported to play a critical role in regulating the carbon pool in soils of the coastal area, as per studies carried out on carbon storage and sequestration in Kadmat Island of Lakshadweep, with reference to *Spinifex littoreus,* a herbaceous plant growing in the coastal sands (Mitra et al. 2017).

Soil fertility status

The soil samples collected from the three islands were of uniform-sized particles of sandy nature and light grey in colour. Samples from lowlands were slightly darker grey than the other sites because of higher organic matter content. Our studies showed the soil pH in the range of 6.6 to 7.5 whereas Krishnan and co-workers (2004) reported pH to be above 8. Reduction in pH could have occurred due to several factors including precipitation, the release of hydrogen ions at the root surface during nutrient uptake and decomposition of the organic matter added by the litter addition (Harter 2007). The inshore and inland soils clearly indicated a neutral pH. Neutral or near neutral pH soils are ideal for plants to easily absorb important nutrients needed for their growth, development and yield (Krishnan et al. 2004).

Soil organic carbon (OC) is critical to soil health and our estimates of high OC content in soils of Lakshadweep is well documented (Singh and Velayudham 1979). OC values obtained in our study were more in confirmation with the values obtained for Kalpeni Island by Krishnan and co workers (2004), compared to higher OC values reported for Minicoy Island by Bhattacharya and co-workers (2008). Nevertheless, it was clear that both the islands were having not less than 2% OC in hinterland soil where bulk of coconut and other vegetation grew. Observation of higher OC in our studies in the interior parts of the islands reflects earlier report in Marshal Islands (Deenik and Yost 2006). Similarly, in coral cay soils from Coral Sea Islands in Australia, soil organic carbon content was reported in the range of 2.4 to 4.8%, 8.09 pH and phosphorus concentration ranging from 467 to 882 mg/kg in the interior portions of the Island. This high fertility was attributed to the availability of large quantities of organic matter falling from the herb-based vegetation in the interior areas of the Island (Batianoff et al. 2010). Thus, the presence of higher range of organic carbon content in the interior parts of coral Islands is a common factor, driven by the litter-shedding taking place from the local vegetation, coconut being the predominant in the case of Lakshadweep islands. Though in our studies, we recorded a slightly lower OC in rhizosphere soils of coconut compared with the general soils, the OC content in Lakshadweep Islands was much higher than the OC content in mainland soils of Kerala (Nair et al. 2018), and other states, where coconut is commonly cultivated (Selvamani and Duraisami 2014; Malhotra et al. 2017). Overall, because of the high above-ground plant biomass density, the carbon accumulation in soil was also significant (Mitra et al., 2017). The superior levels of OC in the soils of the Islands compared to mainland is, therefore, a key factor in higher nut yield and better oil content in the copra of Lakshadweep.

It had been reported that availability of 70–80 ppm mineralizable nitrogen in the basin region is sufficient to meet the N requirements of the coconut palm. About 90% of the N in soil occurs as complex organic forms, accumulated as baseline soil organic matter (SOM), from addition of plant residues, composts, animal manures, etc. which is not directly available to the plants. The organic forms get decomposed/mineralized by the action of soil microbiota to inorganic ammonium (NH_4^+) and ammonium to nitrate (NO_3^-) by nitrifying bacteria, and this contributes significantly to the available N pool required for plants (Sullivan et al., 2020). A recent study in a coconut garden in Mexico had shown that the SOM was highly correlated to plant available NO_3^- (Ramirez-Silva et al., 2021). This supports our hypothesis of availability of sufficient amount of N to coconut palm from the recycled organic matter added to the soil. P concentrations were observed to be lower in inshore and inland samples, the possible reasons could be the ageing of these soils which was reported to reduce the phosphate ions content with time (Nelson et al. 2020), and uptake by vegetation dominated by coconut palms. On the other hand, the high P in the shore soils might be because of regular addition of decomposing phosphate-rich coral skeletons driven by climate change, and nutrient loading from human and fishing activities along the shores (Mallela et al., 2013). Joy and coworkers (2019) had analyzed different phosphorus fractions in the surface sediments collected from shores and lagoons of Lakshadweep islands and reported increasing phosphorus contents compared with previous times. Moreover, the phosphorus present was recalcitrant calcium-bound phosphorus (Ca–P) and not of organic matter origin. The potassium concentrations in most soils were deficient and our values were similar to those in Kalpeni Island reported by Krishnan and coworkers (2004). The second soil analysis of rhizosphere samples of coconut collected from Kalpeni, Minicoy and Kavaratti was restricted to a few parameters. The OC content in the rhizosphere soils of coconut were in midrange between 1 and 2%, whereas available P and K were at higher scale than the site-specific soil analysis data (Table 3). Leaf fall and inflorescence debris around the coconut palms could be the main reasons for this observation. In addition, low sunlight penetration on ground due to profuse and dense canopy on the closely growing coconut palms allowed slow and steady accumulation of the organic matter in the soil due to slow decomposition of the litter. A positive correlation had been reported of the area of litter exposed to light with their decomposition rate (Gallo et al. 2009; Ma et al. 2017). High lignin content in coconut biomass residues was another factor that helped in adding recalcitrant organic carbon to soil under low light intensities. The availability of better P and K to coconut helped in the growth of healthy stand as potassium is critical for plants to evade fungal pathogens. Particulary, in Minicoy, our data on soil fertility was in confirmation with the observations reported in an earlier study, wherein accumulation of organic carbon and aggregation of soil was more pronounced in the central part of the island, and along the eastern shores, which was densely covered with mangrove type vegetation (Vadivelu and Bandyopadhyay 1997). Increase in clay content from the western shore to central islands by 10% is another key reason for the higher OC content in the inland sites, which were also thickly populated with coconut palms (Vadivelu 1979). The trace elements such as Zn, Fe, and Mn were similar to those reported by Gopinath and coworkers (2010), with Zn content increasing in offshore and inland soils. Again, this trace element accumulation had possibly happened because of addition of vegetation as reported in other Islands (Baillie et al. 2021).

Overall, the soil fertility status of the islands seemed adequate for the coconut palm growth and yield, sans any external chemical or other fertilizer application. Near neutral pH, higher OC and reasonable levels of N, P and K availability offered an environment for superior productivity compared to the mainland environment. Soil analysis for NPK contents in Lakshadweep islands indicated that the nitrogen and phosphorus are in substantial supply whereas, 71% of the soils were deficient in K for meeting the demands of crop plants (Krishnan et al. 2004).Thus, per the previous reports and our studies, the key element that needed to be bolstered was potassium. Yet, the coconut palms of Lakshadweep Islands yielded higher than mainland, rarely showed any serious nutrient deficiency or any major disease occurrence even though certain nutrients were observed to be in lower concentrations than required, particularly potassium. It's possible that the balance K was made available by other sources such as fish wastes, seaweeds, sea water and night soil. Seaweeds such as *Ulva* spp. had been reported to be rich in potassium (11.2 mg/l), besides having several nutrients and plant growth promoting hormones (Nasmia et al. 2021). Moreover, Laccadive Ordinary Tall (LCT), the variety predominantly growing in the island, must have developed an excellent adaptation to the Island ecosystem conditions and is able to perform well despite unscientific cultivation practices. However, a thorough study is required to understand the K requirement and its supply to coconut palms in these Islands.

Soil microbial analysis

As most of the Oceanic Islands, including coral islands, are formed de novo without any connection from the mainland (Wolanski 2009), their soil microbial profile is formed by the bacterial and fungal propagules reaching the island through several modes. Primary among them, is the microbiome associated with corals (Ricci 2019), which migrate to soils with degradation of coral skeleton, followed by the propagules arriving by water, air, birds, marine flora and fauna, and human/equipments/sea vehicular movements (McGee 1989). A meticulous soil microbiological study of Lakshadweep islands is lacking and only reports of sponge-associated microbes and their phylogeny (Feby and Nair 2010; Gopi et al. 2012,) are available. A research article on diversity of ACC deaminase bacteria, isolated from the rhizosphere of coconut palms from five different Islands of Lakshadweep (Pandey and Gupta 2020), and a seminar proceedings on prospecting for organic matter degrading bacteria from Amini Island (Menon and Mohan 2016) are the only publications related to agriculture. Higher population of fungi observed in hinterland (inshore and inland) indicated the availability of complex organic residues, which were acted upon and decomposed by this community of microorganisms more aggressively than other communities. Another possible reason reported for the higher fungal population was the habitat heterogeneity (Li et al. 2020) of the island; vegetation heterogeneity was quite evident in the hinterland pockets of the Lakshadweep islands too. Molecular studies on fungal biodiversity in non-coral and coral islands indicated that fungal community assembly was determined by niche-based factors such as host and soil properties and the non-coral soils had higher fungal diversity than coral soils

(Zheng et al. 2021). Presence of reasonable population of fungi in hinterland areas of Minicoy, Kalpeni, and Kavaratti would be critical for microbiological decomposition of the organic matter via production of extracellular enzymes, driving the balance of carbon and plant nutrients, and therefore, playing a critical role in soil health in island soils, as reported in forest soils (Frąc et al. 2018).

Among the function-specific microbiota analyzed in the first set of studies, population of free-living nitrogen fixers, cellulose decomposers and nitrifying bacteria were observed to be higher in the hinterland soil samples compared to shore soils (Suppl. Table 2). However, phosphate-solubilizing bacteria were mostly found in low populations, except in few sites. Contrastingly, populations of both general and function-specific microbial communities in the rhizosphere of coconut were observed to be in significantly higher numbers, in our second set of studies, which included fluorescent pseudomonads and bacilli communities (Table 3). Our observation of high cellulose-degrading microorganisms in the hinterland soils lend support to the fact that an effective decomposition of the lignocellulosic debris accumulating from the coconut palms must be happening to efficiently recycle the nutrients present in these organic residues. While we reported a population of nitrogen-fixing bacteria ranging from 1000 to 10,000 cfu/g dry soil, another research article reported much higher numbers of nitrogen-fixing, P-solubilizing and others in the rhizosphere soil of coconut palm growing in five different islands (Pandey and Gupta 2020). The nitrogen-fixing bacteria, we observed growing in N-free medium, also showed carbonate dissolution to great extent as evidenced by the halo around the colonies (Suppl. Figure 4). High calcium carbonate content is known to enhance the nitrogen-fixing capability of non-symbiotic nitrogen fixing bacteria like *Azotobacter* and others (Ashby et al., 1907). It is possible that the corals soils are rich in non-symbiotic nitrogen-fixing bacteria like *Bacillus* spp., like those of estuary and coastal regions (Yousuf et al. 2017), that have the potential to dissolve and precipitate calcium carbonate (Anbu et al., 2016) and could find possible use in biocementation (Devakumar et al. 2020). Nitrifying bacteria were also recorded in the islands during the first set of studies. Both, nitrogen-fixers that supply nitrogen to plants and nitrifying bacteria that cause loss of nitrogen from the soils, are involved in driving the nitrogen cycle that is crucial to maintain the island ecosystem vegetation. Corals are known to have an association with nitrogen-fixing symbionts and nitrifying bacteria, including prokaryotic and eukaryotic genera (Fiore et al. 2010), which might be contributing such microbiota to the soils of these islands once the coral skeleton degrades and releases the symbiotic microbiota. Though the Lakshadweep soils had low phosphate-solubilizing microbial counts, it was possible that they could be solubilizing phosphorus at higher capacities because of the neutral to alkaline pH of the soils in the islands. A study had indicated that with increase in soil pH, the efficiency and capacities of inorganic phosphate solubilizing bacterial (iPSB) community as well as their abundance increased (Zheng et al. 2019). Moreover, deficiency of phosphate is reported as not a serious problem except in the case of acidic soils where the P ions get fixed in soils (Manicot et al. 1979).

We also found very high populations of fluorescent pseudomonads and bacilli in the rhizosphere soil of coconut, which form the important components of plant growth promoting rhizobacteria (PGPR) in palms (George et al. 2013, 2018). The PGPR promote plant growth directly by production of plant growth promoting hormones and other chemicals, besides a multitude of indirect methods (Gupta et al. 2000; Bhattacharya and Jha 2012). The reporting of large numbers of ACC deaminase producing PGPR from coconut rhizosphere of five Lakshadweep Islands, particularly, *Pseudomonas putida* and *Bacillus paramycoides* as the most effective PGPR based on growth promotion studies with French bean, indicate the role of soil microorganisms in supporting higher yield and productivity of coconut in these coral-based islands (Pandey and Gupta 2020).

Though mycorrhizae association in coconut was first reported by Johnston (1949; Lilly, 1975) from the mainland, our study is the first one to assess the arbuscular mycorrhizal (AM) association status of coconut palms in the Lakshadweep islands. Similar to mainland palms (Ambili et al. 2012), Lakshadweep island palms also had mycorrhizae colonization characterized by arbuscules, vesicles and intraradical hyphae. Paris-type of morphology with compound arbuscules and arbusculate coils was also observed. Based on the spore morphology, arbuscular mycorrhizal fungal genera of *Glomus, Gigaspora, Acaulospora* and *Scutellospora* were identified to be commonly present in the Lakshadweep soils. The highest AM colonization was seen in Kalpeni and Minicoy (61%) and the lowest in Kavaratti (53%). However, spore load was more in Kalpeni (81/10 g) followed by Minicoy (70/10 g) and Kavaratti (63 spores/10 g soil). Simpson's diversity index (Ds) and Shannon's diversity index (Hs) in three different islands (Suppl Fig. 3) indicated that value of "Ds" and "Hs" varied from 0.159 to 0.505 and 0.483 to 1.119, respectively. Arbuscular mycorrhiza fungal species' dominance in Kalpeni Island (0.505, 1.119) was slightly higher than that in Minicoy (0.372, 0.929) and Kavaratti (0.159, 0.483). *Glomus* was the most predominant genus in all the three islands followed by *Gigaspora*. Five different morphotypes of *Glomus* were distributed in Kalpeni Island along with two different morphotypes of *Gigaspora.* In Minicoy, we recorded *Gigaspora* abundance to be on par with *Glomus*. Species richness was less in Kavaratti. It appeared that high-yielding coconut palms had a strong relation with arbuscular mycorrhizhae because similar reports of significantly high AM diversity and population were recorded in coconut palms sampled from Malappuram District of Kerala having the highest yields in whole of Kerala state (Rajeshkumar et al. 2015).

Despite Pearson's correlation coefficient results (Suppl. Table 3) not showing any significant relationship between soil chemical parameters and mycorrhizal parameters, this symbiotic association is known to help the palms in the absorption of nutrients, particularly, phosphorus from a larger distance in soil compared to the roots, and suppression of root pathogens, in addition to their role in the uptake of water under water stress conditions. The mycorrhizal association could be, thus, one of the additional microbial factors that contributed towards the establishment and survival of coconut in nutrient-poor soils and also during drought conditions (Thomas and Ghai 1987). The possibility of mycorrhizhae-driven modulation of drought –induced tolerance genes in plants (Ruiz-Lozano et al., 2006) could not be ignored as one of the reasons for the coconut palms of Lakshadweep to develop tolerance to water-deficit environment, which had been tapped for breeding drought tolerant coconut varieties—Lakshaganga and Chandralaksha (Rajagopal et al. 1990).

Though we did not check for the earthworm population in our studies, Lakshadweep island soils were reported to have earthworm species such as *Pontodrilus laccadivensis* (Beddard 1903), *P. burmudensis.* and *Lampito mauritii* (Haldar et al. 2007). Both *Pontodrilus* spp. and *Lampito* sp. are found in soil with decaying organic matter and salt on seashore and margins of estuaries and brackish water lakes and islands. These earthworms help in the decomposition of the added organic residues; also reported is a rapid transfer of carbon and nitrogen secreted by decomposer soil animals, such as earthworms, to plants (Shutenko et al. 2022). Hence, their role in organic matter decomposition and recycling of nutrients to palms in the island ecosystem needs a thorough study.

Principal Component Analysis

The PCA analysis clearly indicated that the soil organic carbon, organic carbon and potassium added by the autochthonous source of palm litters as well as the arbuscular mycorrhizae spore load in the rhizosphere of coconut palms were strong drivers of the yield of coconut in the island ecosystem. The bacteria, actinomycetes, P-solubilizers and fluorescent pseudomonads were also observed to strongly contribute to the yield of coconut. Actinomycetes are important group of prokaryotes present in abundance, next to bacterial community, in soil (Takahashi and Omura 2003) and are known for carrying out several activities that aid soil health: (i) networking with other soil microbes to break down recalcitrant organic residues to stable humus, (ii) production of antibiotics which help in suppression of pathogenic soil microflora, and (iii) nutrient cycling. Apart from the actinomycetes, pseudomonads, particularly commensal pseudomonad population, in rhizosphere of plants have been proved to induce resistance and disease-suppressive ability thereby promoting good plant health (Mendes et al. 2011; Shalev et al. 2022). Pandey and Gupta (2020) reported several rhizospheric bacteria, including *Pseudomonas* and *Bacillus* spp., isolated from coconut palms of Lakshadweep islands, possessing multiple plant growth promoting traits, in particular the ACC deaminase production capability. The above observations could probably be some of the reasons for the palms being healthy despite growing in extremely dense conditions in the islands. Overall, the autochthonous nutrients added by the palm biomass residues, mineralized by soil microbiota, and microbial symbionts are known to aid in plant growth in nutrient-deficit soils by delivering nitrogen and phosphorus, in barter for the carbohydrate from the plants (Denison and Kiers 2011).

Future perspective

Lakshadweep Island is an ecologically frail ecosystem which is highly sensitive to environmental vagaries and anthropogenic vulnerability (James 2011). The socio-economic development and environmental sustainability of the ecologically fragile Lakshadweep Island will greatly depend on the optimum use of the natural resources, which face increasing rate of degradation influenced by human activities and climate change. Coconut, one of the main sources of income for the inhabitants, will need more scientific cultivation. Conserving the above-ground vegetation and below-ground microbial diversity will play a critical role. The nutrient exhaustion by the vegetation growing in the islands *vis-a-vis* the nutrient addition through return of the organic matter appears to sustain the high yield of coconut as per our study. However, this may not be the complete picture; since, for the positive net primary production in the island, the recycled nutrients alone may not be sufficient even if they are cent per cent efficient. There has to be a new nutrient source that may be acting in the island system (Szmant-Froelich 1983). To address the nutrient input (recycled and new) and the nutrient export balance for sustaining the high coconut yield, a more comprehensive study, involving mapping of the input resources, is required. Further, the role of soil microbiota, as in situ source of new nutrients, and the activities of earthworms, in the overall plant nutrient cycling requires to be investigated using modern molecular tools to help in the development of biofertilizer/bioinoculant technology suitable for maintaining the soil health of the Lakshadweep island ecosystem.

Conclusions

The yield and productivity of coconut palms of Lakshadweep islands, growing without any external fertilizer application, in a forest-like environment, is among the highest in India. We estimated that organic matter residues from coconut palms returned significant amounts of organic carbon, nitrogen, phosphorus, and potassium to the soil. Analysis of general and function-specific soil microbial communities, including arbuscular mycorrhizae, showed that communities such as bacteria, especially *Bacillus* spp., fluorescent pseudomonads, and actinomycetes contributed to major variation in the spatially-relevant sampled sites. The below-ground activities of microbiota would have aided in decomposition, unlocking, and recycling of plant nutrients from the organic matter added by the coconut residues. The recycling of the autochthonous nutrients along with the interplay of the plant–microbe interactions, thus, make the coconut palms survive in natural/organic manner and yield significantly even in the challenging island environment.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11274-022-03373-7.

Acknowledgements The authors sincerely thank the Indian Council of Agricultural Research (ICAR), New Delhi, for funding Network Project on “Application of Microorganisms in Agriculture and Allied Sector (AMAAS)” under which this study was undertaken. Thanks are due to Mr. M.I. Arif, Senior Technician, ICAR-Central Plantation Crops Research Institute, Minicoy (presently with ICAR-Central Island Agricultural Research Institute), for helping in the collection of soil samples at Minicoy, Kalpeni and Kavaratti. The authors are grateful to the anonymous reviewers for their critical comments which helped to improve the ms significantly.

Author contributions MG and AG had conceptualized the hypothesis and the work plan. MG had collected soil samples with the support of technical staff. Vegetation diversity survey was carried out by VA and PMJ. Microbial analysis was carried out by MG and AG, soil physicochemical properties by HPM, and statistical analysis by VA. Manuscript was written by MG, AG and VA with inputs from all authors. All authors reviewed the manuscript.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors declare no conflict of interests.

References

Ambili K, Thomas GV, Indu P, Gopal M, Gupta A (2012) Distribution of arbuscular mycorrhizae associated with coconut and arecanut based cropping systems. J Agri Res. 1(4):338–345

Anbu P, Kang CH, Shin YJ, So JH (2016) Formations of calcium carbonate minerals by bacteria and its multiple applications. Springerplus 5:250. https://doi.org/10.1186/s40064-016-1869-2

Ashby SF (1907) Some Observations on the assimilation of atmospheric nitrogen by free living soil organism *Azotobacter chroococcum* of Beijerinck. J Agr Sci 2:35–51

Baillie IE, Floyd CN, Hallett SH, Andrews R (2021) Topographic and polycyclic pedogenesis in the northern atolls of the Chagos Archipelago, Indian Ocean. Geoderma 26:e00391

Barnes PW, Throop HL, Archer SR, Breshears DD, McCulley RL, Tobler MA (2015) Sunlight and soil–litter mixing: drivers of litter decomposition in drylands. Prog Bot 76:273–302

Batianoff GN, Naylor GC, Fensham RJ, Neldner VJ (2010) Characteristics of coral cay soils at Coringa-Herald Coral Sea Islands. Australia. Pacific Sci 64(2):335–347. https://doi.org/10.2984/64.2.335

Beddard FE (1903) The earthworms of the Maldive and Laccadive Islands. Fauna Geol Maldive and Laccadive Archipel 1:374–375

Bhattacharyya PN, Jha DK (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World J Microbiol Biotechnol 28:1327–1350. https://doi.org/10.1007/s11274-011-0979-9

Bhattacharyya T, Pal DK, Chandran P, Ray SC, Mandal C, Telpande B (2008) Soil carbon storage capacity as a tool to prioritize areas for carbon sequestration. Curr Sci 95:482–484

Biddappa CC, Upadhyay AK, Hedge MR, Palaniswami C (1996) Organic matter recycling in plantation crops. J Plantation Crops 24(2):71–85

Bopaiah MG, Cecil SR (1993) Effect of NPK fertilizers on coconut grown on coral soils of Lakshadweep. In: Nair MK (ed) Advances in Coconut Research and Development. Oxford & IBH Publishing Co Pvt, New Delhi, pp 423–426

Deenik JL, Yost RS (2006) Chemical properties of atoll soils in the Marshall Islands and constraints to crop production. Geoderma 136(3–4):666–681

Denison RF, Kiers ET (2011) Life histories of symbiotic rhizobia and mycorrhizal fungi. Curr Biol 21:R775–R785

Devakumar M, Anand KB, Poornima V, Gopal M, Gupta A (2020) Property enhancement of recycled coarse aggregate using biotreatment approach. Materials Today: Proceedings, https://doi.org/10.1016/j.matpr.2020.10.662

Feby A, Nair S (2010) Sponge-associated bacteria of Lakshadweep coral reefs, India: resource for extracellular hydrolytic enzymes. Adv Biosci Biotechnol 1:330–337. https://doi.org/10.4236/abb.2010.14043

Fiore CL, Jarett JK, Olson ND, Lesser MP (2010) Nitrogen fixation and nitrogen transformations in marine symbioses. Trends Microbiol 18(10):455–463

Frąc M, Hannula SE, Bełka M, Jędryczka M (2018) Fungal biodiversity and their role in soil health. Front Microbiol 9:707. https://doi.org/10.3389/fmicb.2018.00707

Gallo ME, Porras-Alfaro A, Odenbach KJ, Sinsabaugh RL (2009) Photoacceleration of plant litter decomposition in an arid environment. Soil Biol Biochem 41:1433–1441

George M, Anjumol A, George G, Mohamed-Hatha AA (2012) Distribution and bioactive potential of soil actinomycetes from different ecological habitats. African J Microbiol Res. 6:2265–2271

George P, Gupta A, Gopal M, Thomas L, Thomas GV (2013) Multifarious beneficial traits and plant growth promoting potential of *Serratia marcescens* KiSII and *Enterobacter* sp. RNF 267 isolated from the rhizosphere of coconut palms (*Cocos nucifera* L.). World J Microbiol Biotechnol 29:109–117

George P, Gupta A, Gopal M, Thomas L, Thomas GV (2018) Systematic screening strategies for identifying elite plant growth promoting rhizobacteria for coconut (*Cocos nucifera* L.). Int J Curr Microbiol App Sci 7:1051–1074

Gerdemann JW, Nicholson TH (1963) Spores of mycorrhizal endospore species extracted from soil by wet sieving and decanting. Trans British Mycol Soc 46:235–244

Gopal M (2000) Glimpses of coconut cultivation in Andrott Island of Lakshadweep. Indian Coconut J 30(10):1–3

Gopal M, Gupta A, Rajan P, Radhakrishnan Nair CP (2001) Effect of systemic soil insecticides and a plant product on microbial load of soil in root (wilt) affected coconut monocropping ecosystem. CORD 17(1):52–71

Gopi M, Ajith Kumar TT, Balagurunathan R, Vinoth R, Dhaneesh KV, Rajasekaran R, Balasubramanian T (2012) Phylogenetic study of sponge associated bacteria from the Lakshadweep archipelago and the antimicrobial activities of their secondary metabolites. World J Microbiol Biotechnol 28(2):761–766. https://doi.org/10.1007/s11274-011-0860-x

Gopinath A, Nair SM, Kumar NC et al (2010) A baseline study of trace metals in a coral reef sedimentary environment, Lakshadweep Archipelago. Environ Earth Sci 59:1245–1266. https://doi.org/10.1007/s12665-009-0113-6

Gupta A, Gopal M, Tilak KVBR (2000) Mechanism of plant growth promotion by rhizobacteria. Indian J Exptl Biol 38:856–862

Haldar KR, Dhani S, Mandal CK (2007) On some earthworms present in unnamed collections of zoological survey of India. Rec Zool Survey India 107(3):79–93

Hanway JJ, Heidel H (1952) Soil analysis method as used in lowa state college soil testing laboratory. Iowa State Coll Agric 57:1–31

Harter RD (2007) Acid soils of the tropics. ECHO Technical Note, pp 11, http://courses.umass.edu/psoil370/Syllabus-files/Acid_Soils_of_the_Tropics.pdf

Hodge A (2014) Interactions between arbuscular mycorrhizal fungi and organic material substrates. Adv Appl Microbiol 89:47–99. https://doi.org/10.1016/B978-0-12-800259-9.00002-0

IIRS (2010) Biodiversity Characterization at Landscape Level in North West India and Lakshadweep Islands Using Satellite Remote Sensing and Geographic Information System 978–81–211–0774–7, National Remote Sensing Centre, Hyderabad, India

Jackson ML (1973) Soil Chemical Analysis. Prentice Hall of India Pvt. Ltd., New Delhi

Jacob PM, Krishnamoorthy B (1981) Coconut genotypes of Lakshadweep islands. Paper presented in the 4th Plantation Crops Symposium, Mysore, India, 1981. PLACROSYM IV:3–8

James PSBR (2011) Lakshadweep : Islands of ecological fragility, environmental sensitivity and anthropogenic vulnerability. J Coastal Environ 2(1):9–25

Johnston A (1949) Vesicular arbuscular mycorrhizae in sea island cotton and other tropical plants. J Trop Agrl. 26:118–121

Joseph John K, Nair AR, Suma A, Unnikrishnan M, Arunachalam V (2018) Agro-biodiversity and ethnobotany of Lakshadweep Islands of India. Genet Resour Crop Evol 65:2083–2094. https://doi.org/10.1007/s10722-018-0676-8

Jothimani S (1994) Organic farming in coconut. Indian Coconut Journal 25(7):48–49

Joy A, Anoop P, Rajesh R, Mathew J, Mathew A, Gopinath A (2019) Spatial variation of phosphorus fractionation in the coral reef sediments of Lakshadweep Archipelago, Indian. Ocean Chem Ecol 35(7):592–612

Kaladharan P (2001) Seaweed resource potential of Lakshadweep. Geol S India Spec Publ 56:121–124

Kasana RC, Salwan R, Dhar H, Dutt S, Gulati A (2008) A rapid and easy method for the detection of microbial cellulases on agar plates using gram's iodine. Curr Microbiol 57(5):503–507. https://doi.org/10.1007/s00284-008-9276-8

Krishnan P, Nair KM, Naidu LGK, Srinivas S, Koyal A, Nasre RA, Ramesh M, Gajbhiye KS (2004) Land, soil and land use of Lakshadweep Coral Islands. J Indian Soc Soil Sci 52(3):226–231

Li S-P, Wang P, Chen Y et al (2020) Island biogeography of soil bacteria and fungi: similar patterns, but different mechanisms. ISME J 14:1886–1896

Lilly VG (1975) Note on the development of vesicular arbuscular mycorrhiza *Endogone fasciculata* in coconut roots. Curr Sci 44:201–202

Lindsay WL, Norvell WA (1978) Development of a DTPA soil test for zinc, iron, manganese and copper. Soil Sci Soc Amer J. 42:421–428

Lloyd H, Zar KH, Karr JR (1968) On the calculation of information-theoretical measures of diversity [J]. Am mid Nat 79:257–272

Ma Z, Yang W, Wu F, Tan B (2017) Effects of light intensity on litter decomposition in a subtropical region. Ecosphere 8(4):e01770. https://doi.org/10.1002/ecs2.1770

Mandal D, Tripathi KP (2009) Soil erosion limits of Lakshadweep Archipelago. Curr Sci 96(2):276–280

Manciot E, Ollagnier M, and Ochs R (1979) Mineral nutrition of the coconut around the world. Oléagineux. 34:511–515, 576–580

Malhotra SK, Maheshwarappa HP, Selvamani V, Chowdappa P (2017) Diagnosis and management of soil fertility constraints in coconut (*Cocos nucifera*): a review. Indian J Agrl Sci. 87(6):711–726

Mallela J, Lewis SE, Croke B (2013) Coral skeletons provide historical evidence of phosphorus runoff on the Great Barrier Reef. PLoS ONE. https://doi.org/10.1371/journal.pone.0075663

McGee PA (1989) Vesicular-arbuscular mycorrhizal and saprophytic fungi of the Swain Reefs. Australia Mycological Res 93(3):375–378

Mendes R, Kruijt K, deBruijn I, Dekkers E, Van Der Voort M, Schneider JHM et al (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 332:1097–1100. https://doi.org/10.1126/science.1203980

Menon RS, Mohan S (2016) Diversity of Soil Microbes in Amini Island of Lakshadweep, Proceedings of the 25th Swadeshi Science Congress [ISBN: 978–81- 928129–3–9] pp: 382–386.

Mitra A, Sundaresan J, Syed Ali K, Pal N, Datta U, Mitra A, Paramanick P, Zaman S (2017) Baseline data of stored carbon in *Spinifex littoreus* from Kadmath Island, Lakshadweep. In: Goel M, Sudhakar M (eds) Carbon Utilization Green Energy and Technology. Springer, Singapore

Nair KM, Haris A, Mathew J, Srinivasan V, Dinesh R, Hamza H, Subramanian P, Thamban C, Chandran KP, Krishnakumar V, Bhat R, Hegde R, Singh SK (2018) Coconut-growing soils of Kerala: 2. Assessment of fertility and soil related constraints to coconut production. J Plant Crops 46(2):84–91

Nasmia RE, Masyahoro A, Putera FHA, Natsir S (2021) The utilization of seaweed-based liquid organic fertilizer to stimulate *Gracilaria verrucosa* growth and quality. Int J Environ Sci Technol 18:1637–1644. https://doi.org/10.1007/s13762-020-02921-8

Nelliat EV (1973) NPK nutrition of coconut palm. A review. J Plantation Crops, Suppl. 1:70–80

Nelson L-A, Cade-Menun BJ, Walker IJ, Sanborn P (2020) Soil phosphorus dynamics across a holocene chronosequence of aeolian sand dunes in a hypermaritime environment on Calvert Island, BC, Canada. Front for Glob Change 3:83. https://doi.org/10.3389/ffgc.2020.00083

Olsen S, Cole C, Watanabe F, Dean L (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circular Nr 939, US Gov. Print. Office, Washington, D.C.

Ong CS, Juan JC, Yule CM (2017) The contribution of leaching to nutrient release from leaf litter of two emergent tree species in a Malaysian tropical peat swamp forest. Hydrobiologia 794(1):125–137. https://doi.org/10.1007/s10750-017-3086-6

Ouvrier M, de Taffin G (1985) Evolution of mineral elements of coconut husks left in the field. Oléagineux 40(8 & 9):423–430

Pande S, Sant NR, Ranade SD, Pednekar SN, Mestry PG, Kharat SS, Deshmukh V (2007) An ornithological expedition to the Lakshadweep archipelago: Assessment of threats to pelagic and other birds and recommendations. Indian Birds 3(1):2–12

Pandey S, Gupta S (2020) Diversity analysis of ACC deaminase producing bacteria associated with rhizosphere of coconut tree (*Cocos nucifera* L.) grown in Lakshadweep islands of India and their ability to promote plant growth under saline conditions. J Biotechnol 324:183–197

Patil JL, Haldanka PM, Jamadagni BM, Salv MJ (1993) Variability and correlation studies for nut characters in coconut. J Mahrashtra Agrl University 18(3):361–364

Philips JM, Hayman DS (1970) Improved procedures for cleaning roots and staining parasitic and vesicular-arbuscular fungi for rapid assessment of infection. Trans Br Mycol Soc 55:158–161

Rajagopal V, Kasturi Bai KV, Voleti SR (1990) Screening of coconut genotype for drought tolerance. Oléagineux 45:215–223

Rajeshkumar PP, Thomas GV, Gupta A, Gopal M (2015) Diversity, richness and degree of colonization of arbuscular mycorrhizal fungi in coconut cultivated along with intercrops in high productive zone of Kerala, India. Symbiosis 65:125–141

Ramírez-Silva JH, Cortazar-Ríos M, Ramírez-Jaramillo G, Oropeza-Salín CM, Rondón-Rivera DD (2021) Soil organic matter and nitrogen content as related to coconut nutrition in Guerrero. Mexico Open Access Libr J 8:e7727. https://doi.org/10.4236/oalib.1107727

Ratnambal MJ, Nair MK, Muralidharan K, Kumaran PM, Rao EVVB, Pillai RV (1995) Coconut Descriptors Part-I. CPCRI, Kasaragod, pp 168–175

Ricci F, Marcelino VR, Blackall LL, Kuhl M, Medina M, Verbruggen H (2019) Beneath the surface: community assembly and functions of the coral skeleton microbiome. Microbiome 7:159. https://doi.org/10.1186/s40168-019-0762-y

Robertson GP, Paul EA (1999) Decomposition and soil organic matter dynamics. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods of ecosystem science. Springer, New York, pp 104–116

Ruiz-Lozano JM, Porcel R, Aroca R (2006) Does the enhanced tolerance of arbuscular mycorrhizal plants to water deficit involve modulation of drought-induced plant genes? New Phytol 171(4):693–698. https://doi.org/10.1111/j.1469-8137.2006.01841.x

Selvamani V, Duraisami V (2014) Identifying and mapping soil fertility constraints for coconut in Coimbatore and Tiruppur districts of Tamil Nadu state. Indian J Plantation Crops 42(3):348–357

Shalev O, Karasov TL, Lundberg DS et al (2022) Commensal *Pseudomonas* strains facilitate protective response against pathogens in the host plant. Nat Ecol Evol. https://doi.org/10.1038/s41559-022-01673-7

Shameena Beegum PP, Thamban C, Subramanian P, Mathew AC, Ananth PN (2022) Coconut cultivation and coconut based enterprises in Lakshadweep - Changing scenario and need for revitalizing coconut sector. Indian Coconut J 64(9):5–12

Shutenko GS Andriuzzi WS, Dyckmans J, Luo Y, Wilkinson TL, Schmidt O (2022) Rapid transfer of C and N excreted by decomposer soil animals to plants and above-ground herbivores. Soil Biol Biochem. https://doi.org/10.1016/j.soilbio.2022.108582

Simpson EH (1949) Measurement of diversity. Nature 163:688

Singh KD, Velayutham M (1979) Nutrient indexing in coconut leaves and soils of Lakshadweep islands. 1. The need for potash and nitrogen. Indian Coconut J 10(8):1–3

Smith V (2008) Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. Polar Rec 44(3):211–226. https://doi.org/10.1017/S0032247407007218

Soni VK (2021) Long term variation in chemical composition of precipitation and wet deposition of major ions at Minicoy and Port Blair : Islands in Arabian Sea and Bay of Bengal. Mausam 57(3):489–498

Sullivan DM, Moore AD, Verhoeven E, Brewer LJ (2020) Baseline soil nitrogen mineralization: Measurement and interpretation (EM 9281). Oregon State University Extension, Corvallis, OR

Szmant-Froelich A (1983) Functional aspects of nutrient cycling on coral reefs. NOAA Symp Ser Undersea Res. 1:133–139

Takahashi Y, Omura S (2003) Isolation of new actinomycete strains for the screening of new bioactive compounds. J Gen Appl Microbiol 49(3):141–154

Thamban C, Samsudeen K, Shameena Beegum PP (2020) Coconut farming in Lakshadweep Islands - strategies for enhancing sustainability. Technical Bulletin No. 149. ICAR-Central Plantation Crops Research Institute, Kasaragod. p 28

Thomas GV, Ghai SK (1987) Genotype dependent variation in vesicular-arbuscular mycorrhizal colonization of coconut seedlings. Proc Indian Acad Sci (Pl Sci) 4:289–294

Tyagi AP (2009) Solar radiant energy over India. India Meteorological Department, Ministry of Earth Sciences, India, p 4179

Vadivelu S (1979) A hypothesis on the formation of Lakshadweep Islands from pedogenic standpoint. Agropedia 8:1–9

Vadivelu S, Bandyopadhyay AK (1997) Characteristics, genesis and classification, of soils of Minicoy Island. Lakshadweep Indian J Soil Sci 45(6):796–801

Walkley AJ, Black IA (1934) Estimation of soil organic carbon by the chromic acid titration method. Soil Sci 37:29–38

Young HS, McCauley DJ, Dunbar RB, Dirzo R (2009) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. PNAS 107(5):2072–2077. https://www.pnas.org/cgi/content/full/0914169107/DCSupplemental

Yousuf J, Thajudeen J, Rahiman M, Krishnankutty S, Alikunj AP, Abdulla MHA (2017) Nitrogen fixing potential of various heterotrophic *Bacillus* strains from a tropical estuary and adjacent coastal regions. J Basic Microbiol 57(11):922–932. https://doi.org/10.1002/jobm.201700072

Wilkes TI (2021) Arbuscular mycorrhizal fungi in agriculture. Encyclopedia 1(4):1132–1154. https://doi.org/10.3390/encyclopedia1040085

Wilkes TI, Warner DJ, Edmonds-Brown V, Davies KG, Denholm I (2021) Zero tillage systems conserve arbuscular mycorrhizal fungi, enhancing soil glomalin and water stable aggregates with implications for soil stability. Soil Syst 5:4

Wolanski E (2009) Oceans and Aquatic ecosystems Vol II, Encyclopedia of Life Support System. An UNESCO publication. pp 358

Zheng BX, Zhang DP, Wang Y et al (2019) Responses to soil pH gradients of inorganic phosphate solubilizing bacteria community. Sci Rep 9:25. https://doi.org/10.1038/s41598-018-37003-w

Zheng Y, Maitra P, Gan H-Y, Chen L, Li S, Tu T, Chen L, Mi X, Gao C, Zhang G-D (2021) Soil fungal diversity and community assembly: affected by island size or type? FEMS Microbiol Ecology. https://doi.org/10.1093/femsec/fiab062

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com