Marine Pollution Bulletin 209 (2024) 117287

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Challenges to and importance of considering early and intermediate ontogenetic stages in mangrove forest recovery and restoration

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ARTICLE INFO

Keywords:
Mangrove
Sapling
Seedling
Regeneration
Resilience

ABSTRACT

Early to intermediate ontogenetic stages of trees are important in forest regeneration. However, these critical life stages are often overlooked due to survey intensity and impracticality and/or disinterest in characterizing early life stage cohorts. This problem is particularly pervasive in mangrove forests where visibility of smaller stature trees may be limited by tidal flooding and younger cohorts are particularly vulnerable to changing hydrologic and biogeochemical conditions driven by climate change. Lacking data on early life stages in mangrove forests makes it difficult to predict ecosystem degradation and inform habitat resilience and restoration in one of the earth's most valuable blue carbon ecosystems. We identify challenges to collecting empirical data on early to intermediate age classes in mangroves and provide solutions to characterizing these cohorts. We emphasize the importance of gathering these data for improved understanding of forest regeneration dynamics and provide multi-scalar solutions to quantify vegetation structure of mangrove forest.

1. Introduction

An exciting amount of global attention has been dedicated to achieving ambitious goals to restore the world's degraded ecosystems (Lenton et al., 2023). While accomplishing restoration goals in the world's forests depends on interdependent social, ecological, and economic factors, one component is absolutely necessary- new recruits. Ecological theory and restoration practice alike emphasize the need for dispersal and survival of desired plant species as the foundation of ecological sustainability (Palma and Laurance, 2015). Seedlings and saplings, although small in stature, play a disproportionately large role in forest succession. Unfortunately, these young counterparts to the world's forest giants are flying under the radar, both literally and figuratively, and implores the question: are the kids alright?

The importance of quantifying regeneration dynamics to detect early indicators of forest change is universal among forests (Harris et al., 2022), but mangrove forests present a particularly challenging array of barriers, including decreased visibility of lower forest strata due to tidal inundation and propagule loss due to tidal dispersal. Ecological inertia occurs when environmental change decreases or eliminates seedling recruitment, while long-lived mature individuals survive, creating a time lag before ecosystem loss (Smith, 1965). In mangrove forests, survival to maturity is limited by environmental conditions and disturbances during critical lifecycle events (Henderson and Glamore, 2024). Despite the multitude of ecological values mangrove forests provide (e.g., habitat provision (Luther and Greenberg, 2009), shoreline protection (Menéndez et al., 2020), human livelihoods (Zu Ermgassen et al., 2020), and carbon storage and sequestration (Adame et al., 2021)), >20 % of the world's mangrove areas have been degraded or lost since the mid-20th century (Duke et al., 2007; Friess and Webb, 2014) and trends remain at a net loss (Goldberg et al., 2020; Bunting et al., 2022). The need for restoration of these ecosystems is urgent, but too often restoration efforts are characterized by poor survival of planted propagules (Rodríguez-Rodríguez et al., 2021). Data-informed guidelines are needed to meet mangrove ecosystem goals (Rodríguez-Rodríguez et al., 2021), particularly as climate change related disturbances (e.g., tropical cyclones) alter ecosystem structure and function (Amaral et al., 2023). Although the recovery of mature mangroves following cyclones has

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https://doi.org/10.1016/j.marpolbul.2024.117287
Received 10 June 2024; Received in revised form 8 November 2024; Accepted 8 November 2024

increasingly been studied (Peereman et al., 2022; Mo et al., 2023), regeneration dynamics following disturbances remain poorly understood.

Mangrove research and restoration guidelines to date largely focus on two life stages: 1) propagule dispersal and initial seedling establishment and 2) the distribution, extent, and structure of mature adults. Intermediate ontogenetic stages (i.e., seedlings and saplings) are underrepresented in mangrove research (Sloey et al., 2022) even though tree seedling mortality rates are widely recognized as an important limitation on reforestation (Keeton, 2008). Understanding the factors that limit survival of mangrove propagules is crucial to modeling forest condition and development, forecasting forest recovery, informing human-aided management efforts (Kamali and Hashim, 2011), and presents opportunities for scientific inquiry. Here, we 1) identify challenges to collecting empirical data on young trees, 2) demonstrate the value of early to intermediate life stages to understanding mangrove forest regeneration and restoration dynamics, 3) provide solutions to characterizing intermediate aged cohorts, and 4) provide recommendations to guide future research.

2. Challenges to collecting empirical data on early and intermediate life stages

The delineation of mangrove life stages is predominantly based on size, and largely generalized considering interspecies variation in propagule length. For example, propagule length ranges from <1.5 cm in *Laguncularia racemosa* and *Avicennia germinans* (Sousa et al., 2003) to ~45 cm in *Rhizophora mucronata* (De Ryck et al., 2012). Krauss et al. (2008) defined a mangrove seedling as a rooted individual and saplings as trees ~1 m tall. Radabaugh et al. (2020) described mangrove seedlings as individuals with stem height < 1 m, saplings with height > 1 m and DBH < 5 cm, and adult trees as having a DBH > 5 cm. Defining ontogenetic stage by size class is informative for describing forest structure, but species and regional specific refinement of these classes is necessary. Using a single size class to categorize all seedlings/saplings over-simplifies an important continuous variable (size), which has been shown to predict seedling survival in other forested ecosystems (McWilliams et al., 2015; Vickers et al., 2019).

Many forestry sampling protocols delineate a minimum diameter class, excluding sapling and seedling cohorts (Lugo and Snedaker, 1974). Mangrove seedling and sapling dynamics are generally only the focus of studies when larger trees are absent (Krauss et al., 2020), in restoration contexts (Lewis III et al., 2016), or when mangroves encroach into other ecosystems (Charles et al., 2020; Yando et al., 2021). Due to the logistical demands of quantifying seedlings and saplings, studies that focus on these age classes are generally restricted to small spatial areas. Though small plots can be scaled up to larger spatial scales, the heterogeneity inherent to seedling establishment (Nicotra et al., 1999) introduces potential for greater inaccuracies when scaled up (Harris et al., 2022). Seedlings are often short-lived with dynamic species-specific phenology (Clarke and Allaway, 1993; Yando et al., 2021), making them difficult to quantify and track over time or determine the dominant cause of loss. Seedling and sapling information may be included in more comprehensive long-term mangrove studies (i.e., Rivera-Monroy et al., 2019), but it is rarely the focus.

Modeling and remote sensing have improved our understanding of mangrove dynamics on local to global scales (Giri et al., 2011; Simard et al., 2019; Lagomasino et al., 2021). Because large-scale mangrove mapping efforts inherently rely on passive remote sensing imagery (Campbell et al., 2022), seedlings and saplings are hidden. Numerical models have characterized global-scale dispersal dynamics for mangrove propagules (Van der Stocken et al., 2019), but studies on seedling or sapling survival at comparable spatial scales do not exist. Recent efforts have been able to resolve below canopy structure gaps using lidar sensors from airborne (Xiong et al., 2022; Chavez et al., 2023), unmanned aerial vehicle (UAV) (Yin and Wang, 2019), and terrestrial platforms (Willim et al., 2019). Unfortunately, visual and remote sensing observation of seedlings is further limited by tidal stage and timing of imagery.

3. Cause for characterizing seedlings and saplings

Quantifying early to intermediate life stages of mangroves is needed to improve conservation efforts, anticipate forest degradation/resilience (Fig. 1), and understand their contribution to ecosystem function and succession. Many mangrove species are viviparous or cryptoviviparous, thus establishment is facilitated by initial energy reserves. As the plant transitions to photomorphogenesis, establishment does not guarantee survival. Thus, the presence of propagules does not equate to mangrove ecosystem restoration (Lewis III et al., 2016). Seedling and sapling survival serves as a better indicator of appropriate ecological conditions. Their growth drives rapid functional rebounds of biomass and carbon following disturbance, thereby contributing to forest recovery (Odum, 1969; Barr et al., 2012).

Most human-aided mangrove plantings use propagules, despite

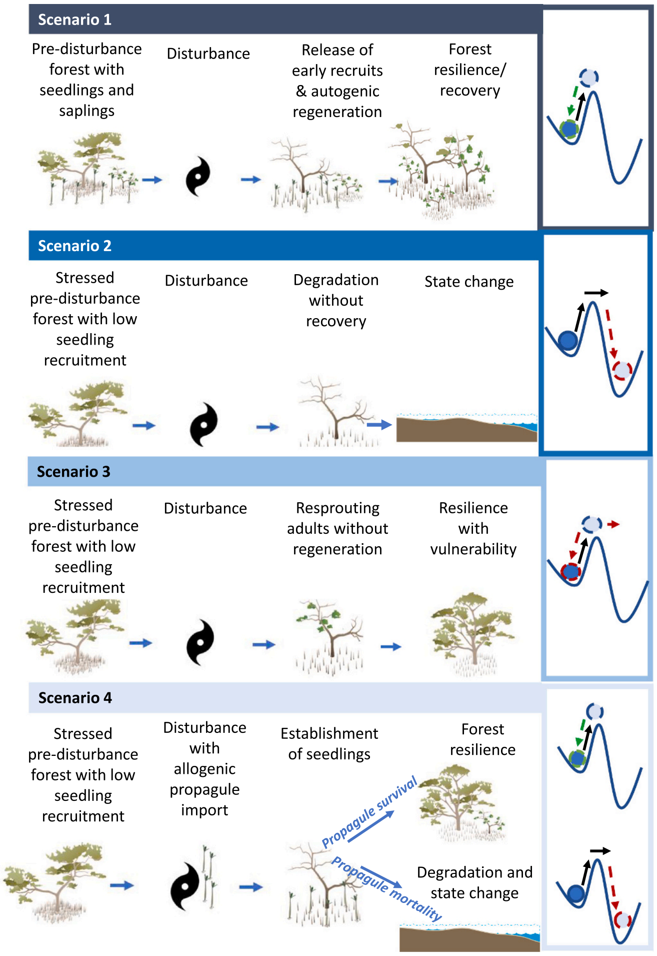

Fig. 1. Conceptual model showing the influence of young cohorts on ecosystem recovery following a disturbance under four scenarios plotted alongside corresponding stable state ball and cup conceptual models. Scenario 1: The existing cohort of young recruits facilitate recovery following disturbance. Resilient mature trees resprout after damage and saplings and seedlings recruit into larger size classes. Scenario 2: Lack of the young cohort prevents forest resilience and recovery post-disturbance resulting in degradation and state change. Scenario 3: Resprouting of resilient mature trees facilitates recovery, but the system remains vulnerable due to lack of young cohort. Scenario 4: Allogenic propagules may contribute to recovery. However, if allogenic propagules do not survive due to inopportune establishment conditions, the system will degrade.

survival of planted propagules generally being low (Clarke and Kerrigan, 2002). The ease of propagule harvesting and planting differs by species due to morphometrics, resulting in a bias toward *Rhizophora* spp. (Hai et al., 2020). A less common technique involves rearing trees to a more robust sapling stage before transplanting (Chowdhury et al., 2019), which may increase chance of survival, but also increases financial investment. Self-design restoration approaches may instead focus on restoring the proper abiotic conditions for natural propagule recruitment, a technique that has shown promising results (Djamaluddin et al., 2023; Sánchez-Núñez et al., 2023).

Early to intermediate life stages better represent current ecosystem status than established adult trees (Huston and Smith, 1987), and thereby can serve as an early warning system for a forest's potential to regenerate following a disturbance (Fig. 1). For example, a mangrove complexity index, a measure combining species richness, basal area, maximum height, and stem density (Holdridge et al., 1971), has been implemented to predict vulnerability to "mangrove forest heart attacks" by integrating historic conditions in the canopy layer and current conditions in the understory (Lewis III et al., 2016). Limited seedling and sapling availability before a disturbance can indicate stressed abiotic conditions (Lewis III et al., 2016), whereas sapling and seedling mortality after a disturbance may indicate detrimental biogeochemical changes driven by the disturbance itself (Salmo et al., 2014; Lagomasino et al., 2021; Radabaugh et al., 2020). An influx of propagules from neighboring populations following a disturbance may influence forest recovery, but without prior quantification of propagule, seedling, and sapling communities it may be impossible to detect if recovery was autogenic or allogenic (Fig. 1). Apparent recovery following a disturbance is also not necessarily indicative of forest sustainability. For example, mature trees in storm-damaged forests may resprout (apparent recovery), but without retention of young cohorts in newly exposed canopy gaps, the system will remain vulnerable to future disturbances when mature trees succumb to stress (Fig. 1).

Developing better approaches to capturing early growth stage dynamics will improve predictions of system-wide resilience. For instance, long-term mangrove studies as part of the Florida Coastal Everglades Long-Term Ecological Research program have provided observations of mangrove ecosystem recovery in response to hurricanes and sea level rise at the regional scale (Castañeda-Moya et al., 2013, 2020; Danielson et al., 2017; Rivera-Monroy et al., 2019; Zhao et al., 2021). Spatiotemporal patterns in mangrove demography in permanent plots in the southwestern Everglades have been analyzed over a ~20 year period (2001−2020), during which two cyclones passed over the region, Hurricanes Wilma (2005) and Irma (2017) (Rivera-Monroy et al., 2019). By measuring trees in size classes with DBH $\geq$ 2.5 cm, this study was able to quantify increases in aboveground biomass and basal area post-hurricane Wilma (2005). After the storm, the less-severely impacted upstream site showed that smaller tree cohorts (DBH 2.5–5 cm) grew into larger trees, replacing biomass lost during the storm and contributing to a resilient overall vegetative structure (Castañeda-Moya et al., 2013; Rivera-Monroy et al., 2019). Moreover, permanent mangrove vegetation plots surveyed before (2015) and after (2020) the passage of Hurricane Irma (2017) revealed an overall significant reduction in total basal area at all mangrove sites, but a significant increase in basal area of smaller trees (DBH 2.5–5 cm) (Castañeda-Moya et al., unpublished data), suggesting rapid recruitment of juvenile saplings into adult cohorts despite the high tree mortality. But plots established in a degraded mangrove forest after Irma (2020), showed no signs of recruitment or small trees (Lagomasino et al., unpublished data). These results underscore the temporal patterns in tree recruitment in response to a disturbance event, but without long-term monitoring of smaller age classes, it is difficult to determine the underlying cause of recruitment and recovery.

4. Solutions for data collection challenges

4.1. Field studies

So how do we gather information on early to intermediate mangroves? Generally, research focused on these life stages is conducted in greenhouse or mesocosm experiments or small scale field-based studies. Extrapolating these studies to make robust models has limitations, but nevertheless informs understanding of processes at larger scales. For example, Sloey et al. (2022) tracked survival of >3000 mangrove seedlings for a full year on a ~10km^2 island in southeast Asia.The large sampling size of seedlings, and intensive reoccupation of plots, across this small area served to inform mangrove seedling survival more broadly. When seedlings are not directly measured in the field, environmental parameters can be used to surmise mangrove seedling success. For instance, Fitri et al. (2019) monitored the development of soil nutrients in Carey Island, Malaysia to determine the point at which soil development would support mangrove establishment.

Unfortunately, the need for quantification of early life stages is often only realized after a disturbance; by that time monitoring will have missed important prior forest demography. We encourage rapid sampling of early life stages in all long-term forest surveys of incorporation of permanent plots in which seedlings and saplings are more intensively sampled. Even simple seedling tallies and/or species identification in subplots would be immensely valuable. If these data are currently being collected, they are not being made as accessible as larger size-class community data. Relatively few studies assessing hurricane effects on mangrove forests have focused on development of early and intermediate mangrove life stages pre- or post-hurricane (Sherman et al., 2001; Radabaugh et al., 2020). The few studies that do have revealed important differences in species-specific persistence of seedlings along abiotic gradients (Ellison and Farnsworth, 1993), and the role persisting seedlings play in rapid ecosystem recovery (Krauss et al., 2023). The USDA Forest Service's Forest Inventory and Analysis program demonstrated the utility of refined tree seedling measurements to predict tree mortality and forest succession throughout US forests (McWilliams et al., 2015). The regeneration indicator dataset produced through this program is a potential model for global mangrove forest surveys and other forest types alike.

4.2. Remote sensing techniques

Scaling up characterizations of forest seedling/sapling dynamics to landscape or global spatial scales will require more than on-the-ground surveys. Remote sensing techniques, such as Normalized Difference Vegetation Index (NDVI) time series analyses have a longer history of providing large scale assessments of forest recovery or restoration across larger spatial scales (Green et al., 1998; Cabello et al., 2021; Suwanto et al., 2021), but the resolution of these analyses lack the refinement to understand the complexity of forest change or detect vulnerability to future state change (Fig. 1). Fortunately, lidar remote sensing techniques have made strides in measuring the lower forest strata (Li et al., 2021), and is being used to study mangrove recruitment, canopy regrowth, and resilience following hurricane disturbances (Lagomasino et al., 2021; Xiong et al., 2022; Chavez et al., 2023) (Fig. 2). NASA Goddard's Lidar, Hyperspectral and Thermal (G-LiHT) imager airborne Lidar (Cook et al., 2013) was used to collect high density point clouds of mangrove forests in the Florida Everglades following Hurricane Irma in 2017. Digital Surface Models (DSM), Canopy Height Models (CHM), and height percentiles derived from these point clouds before and after the hurricane showed significant damage to the forest's lower strata (Xiong et al., 2022). Global Ecosystem Dynamics Investigation (GEDI), launched in December 2018, is another emerging technology (Dubayah et al., 2020) that uses lasers that can penetrate through forests and map the 3D lower strata structure (Fig. 2). From the GEDI products, metrics including Plant Area Index, Plant Area Volume Density, ground elevation, canopy

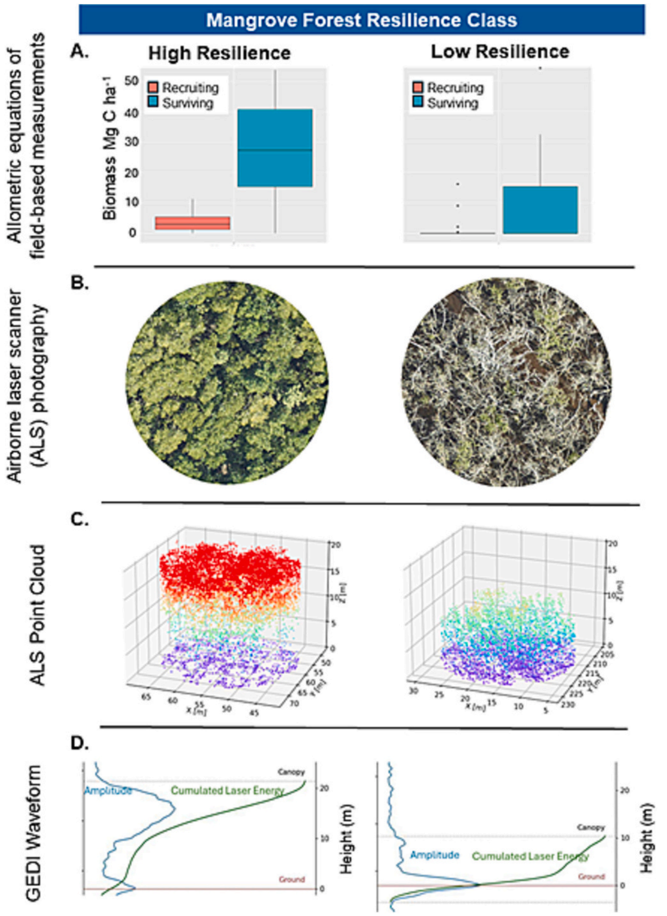

Fig. 2. Contribution of young cohorts to forest recovery post-disturbance measured in high and low resilience mangrove forest plots using four approaches that vary in scale and detection precision. (A) Aboveground biomass of surviving mangrove trees (dbh >5 cm) (turquoise) and mangroves that recruited from smaller size classes (coral) following disturbance estimated from field-based measurements. (B) Photography derived from airborne laser scanner (ALS) showing differences in emergent and canopy forest structure between high resilience plots and defoliated low resilience plots. (C) Point cloud derived from ALS photography showing greater information and detail on lower forest strata. (D) Waveform of the GEDI shot in mangrove forests. Forest structure including top canopy, lower strata vegetation, and ground can be characterized by the waveform. Plant Area Volume Density (PAVD) (m^2/m^3) can quantify the vertical structure of forest by calculating plant area per unit volume. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

height, and relative height (RH) metrics can be obtained, providing information about forest complexity (Yun et al., 2023). Future NASA lidar mission, the Earth Dynamics Geodetic Explorer (EDGE), will use full waveform lidar with swath-mapping capability to monitor the global ecosystem with better data coverage. These spaceborne lidar missions shows promise for large scale remotely sensed quantification of lower strata mangrove vegetation biomass.

5. Summary

Increased attention on historically understudied ontogenetic stages of mangroves is needed to understand species-specific biology and improve predictions of the fate of forest recovery after disturbances. Moreover, this information could be used as early warning systems to identify vulnerable regions. Regardless of forest management, or disturbance recovery response, the continued sustainability of mangrove forests depends on the young and intermediate life stage cohorts. With advancements in technological capacities and ease of incorporating seedling/sapling monitoring into field studies, there is no excuse to ignore these critical stages. Ultimately, the need to understand these life stages is not limited to mangroves, but rather provides ecological/basic science with a greater understanding of areas that are often lumped into the "black box" of community ecology (Vellend, 2010). The kids are alright, but it's time we pay more attention.

CRediT authorship contribution statement

Taylor M. Sloey: Writing – review & editing, Writing – original draft, Visualization, Supervision, Investigation, Conceptualization. **Sean P. Charles:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization, Visualization. **Lin Xiong:** Writing – review & editing, Visualization, Conceptualization. **Edward Castañeda-Moya:** Writing – review & editing, Investigation. **Erik S. Yando:** Writing – review & editing, Investigation, Conceptualization. **David Lagomasino:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Conceptualization.

Author contributions

All authors contributed to the conceptualization and editing of the manuscript. TMS and DL wrote the manuscript. TMS created Fig. 1; SPC and LX created Fig. 2.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Ethics approval

Not applicable.

Funding

DL and SPC were supported in part by NASA Carbon Monitoring Systems (Grant No. 80NSSC21K1564). The FCE-LTER program funded by the National Science Foundation (Grant #DEB-2025954) and the Department of the Interior – The National Park Service / Everglades National Park (CESU Cooperative Agreement #P18AC00974 Task Agreement # P20AC00547) provided partial funding for E C-M.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Special thanks to the Everglades National Park for granting research permits and the Florida Bay Interagency Science Center-Everglades National Park (FBISC-ENP) for logistic support during the study. This is contribution number 1785 from the Institute of Environment at Florida International University.

Code availability

Not applicable.

Data availability

Data presented in Fig. 2A is a subset of a larger dataset (Radabaugh et al., 2023) archived online through the Smithsonian Environmental Research Center (doi:10.25573/serc.23960826.v1). High resolution area photos (Fig. 2B) are available through the G-LiHT websites: (https://glihtdata.gsfc.nasa.gov/files/G-LiHT/FL_20170328_Harney_River/photography/orthomosaic/FL_20170328_Harney_River_l0s3_ortho.tif), and (https://glihtdata.gsfc.nasa.gov/files/G-LiHT/FL_20171206_FIA8/photography/orthomosaic/FL_20171206_FIA8_l0s9_ortho.tif). Airborne lidar data (Fig. 2C) is available through G-LiHT websites: (https://glihtdata.gsfc.nasa.gov/files/G-LiHT/FL_20170328_Harney_River/lidar/las/FL_20170328_Harney_River_l0s3.las.gz) and (https://glihtdata.gsfc.nasa.gov/files/G-LiHT/FL_20171206_FIA8/lidar/las/FL_20171206_FIA8_l0s9.las.gz)). The waveform and rh metrics data (Fig. 2D) is extracted from GEDI L1B product from NASA's Land Processes Distributed Active Archive Center (LP DAAC): (https://e4ftl01.cr.usgs.gov/GEDI/GEDI01_B.002/2021.09.08/GEDI01_B_2021251024134_O15513_02_T04789_02_005_02_V002.h5), (https://e4ftl01.cr.usgs.gov/GEDI/GEDI02_A.002/2021.09.08/GEDI02_A_2021251024134_O15513_02_T04789_02_003_02_V002.h5), (https://e4ftl01.cr.usgs.gov/GEDI/GEDI01_B.002/2019.12.02/GEDI01_B_2019336024706_O05499_03_T03754_02_005_01_V002.h5), and (https://e4ftl01.cr.usgs.gov/GEDI/GEDI02_A.002/2019.12.02/GEDI02_A_2019336024706_O05499_03_T03754_02_003_01_V002.h5).

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