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Review

Emerging Forest Diseases: A Case Study of Greenheart (*Chlorocardium* spp., Lauraceae) and the Newly Described Fungus, *Xylaria karyophthora*

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Abstract: Greenheart (*Chlorocardium* spp., Lauraceae) is one of Guyana's most economically important timber species. It is a large evergreen canopy tree with desirable wood characteristics and no previously recorded pathogens. Recently, however, the fungal species *Xylaria karyophthora* was described from morbid Greenheart seeds found throughout central Guyana. For years, forestry stakeholders have postulated that the future of Greenheart in Guyana is threatened due to overharvesting. However, *X. karyophthora* may represent a new immediate threat to the Greenheart industry. The exact time of emergence of this fungus is unclear, although our examination of historical records indicates that it was sometime before 2000. In this review, we discuss the history of key silvicultural and mycological research in relation to Greenheart in Guyana and the threats to its production.

Keywords: Guiana shield; Guyana; new diseases; seed colonist; *Xylaria*; Xylariaceae

1. Introduction

The largely pristine forests of Guyana cover 76.6% (16.5 million hectares) of the total land area [1]. The majority of Guyana's forests are mixed with a floristic diversity that is little exploited for timber [2], yet 8.7 million hectares are considered accessible for exploitation. In fact, deforestation rates in Guyana are among the lowest in the world, between 0.02% and 0.08% per annum over the last two decades [3]. The most economically valuable timber species include Mora (*Mora excelsa* Benth. and *M. gonggrijpii* (Kleinhoonte) Sandwith), Baromalli (*Catostemma commune* Sandwith), Purpleheart (*Peltogyne* spp. Vogel), Crabwood (*Carapa guianensis* Aubl.), Kabukalli (*Goupia glabra* Aubl.), and Greenheart (*Chlorocardium* sp. Rohwer, H.G. Richter and van der Werff) [4]. The genus *Chlorocardium* consist of two species, *C. rodiei* (Schomb.) Rohwer, H.G. Richter and van der Werff and *C. venenosum* (Kosterm. and Pinkley) Rohwer, H.G. Richter and van der Werff, with *C. rodiei* (Greenheart) being one of the main pillars of the forestry industry in Guyana [5].

The logging and sale of Greenheart are among the oldest activities of Guyana's forestry sector. Until 1997, Greenheart was the largest contributor to gross and export revenue from timber sales [5,6]. Today, it remains one of the most merchantable timber products [5], as it is world-renowned for its exceptional qualities. Greenheart is durable, resistant to biodegradation under saline conditions, impervious to damage by termites and marine crustaceans, and resistant to fire [7,8]. For these reasons, Greenheart wood is especially valuable in numerous maritime applications as well as a wide range of other uses such as in housing construction, heavy furniture, turnery, and fishing rods [5].

Among the major threats to Guyana's forests in general, and by extension Greenheart species, are mining and overharvesting [9,10]. However, the very recent discovery and documentation of *Xylaria* *karyophthora* Husbands, Urbina & Aime, a putative pathogen of the seeds of *Chlorocardium* spp., may present a new and emerging threat to the Greenheart industry in Guyana [11].

2. Greenheart (*Chlorocardium* spp.)

Species of *Chlorocardium* (Lauraceae) are endemic to South America and occur almost exclusively in Guyana but can also be found in Venezuela and Suriname in low densities [12]. The trees are distributed in mixed evergreen forests in varying densities on sandy soils of the Berbice formation, which extends from the central to the eastern part of the country [13]. The Bartica Triangle, which occupies a central position within the confluence of the Essequibo, Cuyuni, and Mazaruni Rivers and surrounding forest contain some of the highest densities of Greenheart-dominated stands [13,14].

Species of *Chlorocardium* are large, long-lived, evergreen canopy trees [9,15,16]. These species are characterized as shade tolerant [9], but seedlings respond well to open gaps in the forest canopy [6]. The trees can reach heights of 27.4–39.6 (49) m with stem diameters between 0.35–0.6 m [9,14]. Peak flowering and fruiting occurs annually from March to May, and fruit maturation takes approximately one year [9,14,15]. The fruit is a single seeded drupe that undergoes prolonged dormancy after barochorous dispersal. Mast fruiting occurs every 12–15 years [14,17] and the seeds are known to contain numerous secondary alkaloids that protect them from predation and disease [18]. Although the seeds are known to be attacked by some pre- and post-dispersal invertebrates (e.g., *Stenoma catenifer* Walsingham; *Cladoctonus* spp.) and rodents (e.g., *Dasyprocta* spp.) [19–21], attacks by seed pathogens are largely unknown.

This species was first commercialized during the late 18th century and dominated timber trade between 1954 and 1975 [7]. Due to the heavy commercial reliance on Greenheart timber, there has always been a reoccurring uneasiness concerning threats from over-exploitation [22–24]. Given the importance of Greenheart to the Guyanese economy, any threat to this species is also a threat to the Guyanese economy. However, these concerns abated somewhat in the 1920s and 1940s with the uncovering and accessing of vast expanses of primary forest due to the shift from manual to mechanized extraction techniques. In the 1950s and 1960s, the construction of roads and the utilization of more modernized equipment for harvesting, stumping, and transportation of extracted logs allowed for improved access and exploitation of remote forest areas [7]. In addition to the gradual encroachment into these primary forests, there was also a thrust towards the establishment of policies for sustainable forest management [24–26]. The push for sustainable forest management resulted in more than a century of silvicultural, ecological, mycofloristic, and mycological research as well as numerous surveys spanning a wide range of forestry issues. Many of these studies emphasized aspects of sustainable management for Greenheart as a means to ensure future viability of this species [13,27–30].

3. Key Silvicultural Findings on Greenheart from Guyana

Davis and Richards [8] in their work on the vegetation of Moraballi Creek in Guyana established 122 m^2 plots in five forest types viz. Mora (*Mora excelsa*), Morabukea (*M. gonggripii*), Wallaba (*Eperua* spp. Aubl.), Greenheart (*Chlorocardium* spp.), and mixed forest, to assess their floristic composition. The study was carried out in primary forest and the results showed a smaller count of trees in the lower size class for Greenheart when compared to other species. The authors reported that this phenomenon is a constant feature in Greenheart forests and described it as being "curious", since the presence of small saplings below 100–200 cm was fairly abundant. This study, however, never assessed factors that might be responsible for the low observed Greenheart population in the lower class-sizes. Further, it is important to note that during the period of this investigation, there appeared to be no negative impact on seedling recruitment, as the authors recorded high seedling (young tree less than 1 inch in diameter) counts for Greenheart within the plots.

The work of Fanshawe [31], documenting trees of British Guiana, reported that germination of Greenheart seeds in natural stands was at about 90%. This work also posited that Greenheart was not considered a candidate for plantation establishment because natural regeneration was abundant.

Fanshawe also highlighted that regeneration could be successfully supplemented by broadcasting seeds, transplanting seedlings, and manipulating the canopy and understory by poison-girdling to improve illumination that favors germination.

Due to the economic importance of Greenheart and prevailing fears that overharvesting could impact future sustainability of this species, there were recommendations from the World Bank Missions to then British Guiana in 1953 to commence regeneration in worked-out Greenheart forest. The then Guiana Forest Department conducted a series of experiments to determine conditions that favor Greenheart regeneration. A pilot project commenced in 1954 and covered 2.59 km^2 of exploited forest in the Bartica Triangle. The area was divided into 48 ten-acre compartments with different treatments. The results, commonly referred to as the EC Clarke report, were published in 1956 and, for example, showed that after 94 stumps of commercial trees were removed, there remained large populations of trees 8 inches in diameter and above, saplings (young tree of diameter 1–5 inches) below eight inches in diameter, and seedlings to saplings below ten feet high. The report also indicated that regeneration was better in compartments treated by manipulating the canopy or understory to increase light conditions.

Hammond and colleagues [21] examined the spatial and temporal patterns of seed attack and germination in large-seeded Neotropical trees with specific reference to *Chlorocardium* species. They showed that despite a large number of attacks by invertebrates and rodents, greater than 60% of all seeds (pooled n = 480) in the control had established a radicle by 85 weeks, and an additional 10% formed a radicle where treatments of insecticide plus cage were applied. Subsequently, greater than 79% shoot formation occurred in all treatments with rooted individuals. The silvicultural and ecological work of Davis and Richards [8], Hammond [21], the EC Clarke report [24], or Fanshawe [31] or did not recognize any constraint to Greenheart seed germination and recruitment from seed pathogenic fungi and no major threat to seed viability for this species.

4. Common Threats to Greenheart Populations in Guyana

Mining and overexploitation of forest resources are among the major threats to forest degradation and deforestation [10,12]. Nevertheless, the overexploitation of Greenheart forests in particular and its impact on the future sustainability of this species has been a concern for stakeholders since the late 1800s [22–24]. There are other factors that have had minimal effect on Greenheart seed viability. Early silvicultural investigations by Fanshawe [31] also indicate mammalian predation, with the attacks occurring primarily under conditions where more palatable seeds are unavailable. He also indicated that seeds can readily lose viability in the presence of unfavorable abiotic conditions, however, damages from the aforementioned sources were not significant enough to affect favorable seedling recruitment, and likewise, no evidence for increased herbivory or environmentally caused loss of viability were observed. The work of Hammond [21] also echoed similar sentiments highlighting that a large percentage of the artificially dispersed Greenheart seeds were attacked primarily by insects such as Scolytidae beetles of the genus *Sternobothrus* Eggers and species of the fungus-feeding ants *Trachymyrmex* Forel and *Sericomyrmex* Mayr as well as the microlepidopteran, *Stenoma catenifer*. Further, small rodents of the Dasyproctidae family were also reported to feed on the seeds of Greenheart. It is widely known that seed mortality is principally due to pre- and post-dispersal attack by invertebrates, vertebrates, and pathogens as well as unfavorable abiotic factors [32–34] and that this can have major influences on the propagative success, population spatial patterns, and community diversity of tree species [35–37]. Nevertheless, none of the aforementioned herbivory studies reported major negative influence on seed viability of Greenheart.

5. *Xylaria karyophthora*: Discovery of a Putative Pathogen of Greenheart Seeds

Silvicultural and ecological records for decades continually revealed the absence of seed-associated parasites/pathogens of Greenheart. However, in 2011 we observed numerous black fungal fruiting bodies emerging directly from dead Greenheart seeds in logged and unlogged forest of central Guyana (Figure 1). This fungus was subsequently described as *Xylaria karyophthora* [11]. Extensive field studies undertaken in 2011 and 2015–2016 indicated this new species of *Xylaria* was aggressively colonizing and producing fruiting structures on the cotyledons of ca. 80% of dispersed seeds from both species of *Chlorocardium* in Central Guyana. However, the life history strategy of this fungus is unclear and therefore will necessitate intensive investigations to understand its biology, ecology, and epidemiology. Further, the impact of this fungus on Greenheart seedling recruitment also needs to be addressed, since regeneration of Greenheart is directly by seeds.

There are less than 30 recognized species of wild fruit- and seed-inhabiting *Xylaria* from both temperate and tropical systems. This is a small fraction of the more than 1300 accepted species within the genus [38], but this low number may not necessarily indicate low diversity, but rather, this group might be largely under-investigated. San Martin and Rogers [39] documented *X. magnoliae* J.D. Rogers, *X. carpophila* (Pers.) Fr., and *X. persicaria* (Schw.: Fr.) Berk. & Curt. as saprobes of the fruits of *Magnolia grandiflora* L., *Fagus* sp., and *Liquidambar formosana* Hance, respectively. These are generally considered temperate species. *Xylaria ianthinovelutina* (Mont.) Fr. and *X. culleniae* Berk. & Broome colonize leguminous species from tropical regions [40,41]. Yu-Ming et al. [42] recently presented the most comprehensive documentation of 25 fructicolous and seminicolous *Xylaria* species based on morphological characteristics. Most of these fruit- and seed-inhabiting *Xylaria* are generally thought to be host restricted even though the reason for their preference is unclear [42]. Many of them are only known from the type specimen and considerable data are lacking regarding their biology, mode of infection, and epidemiological potential.

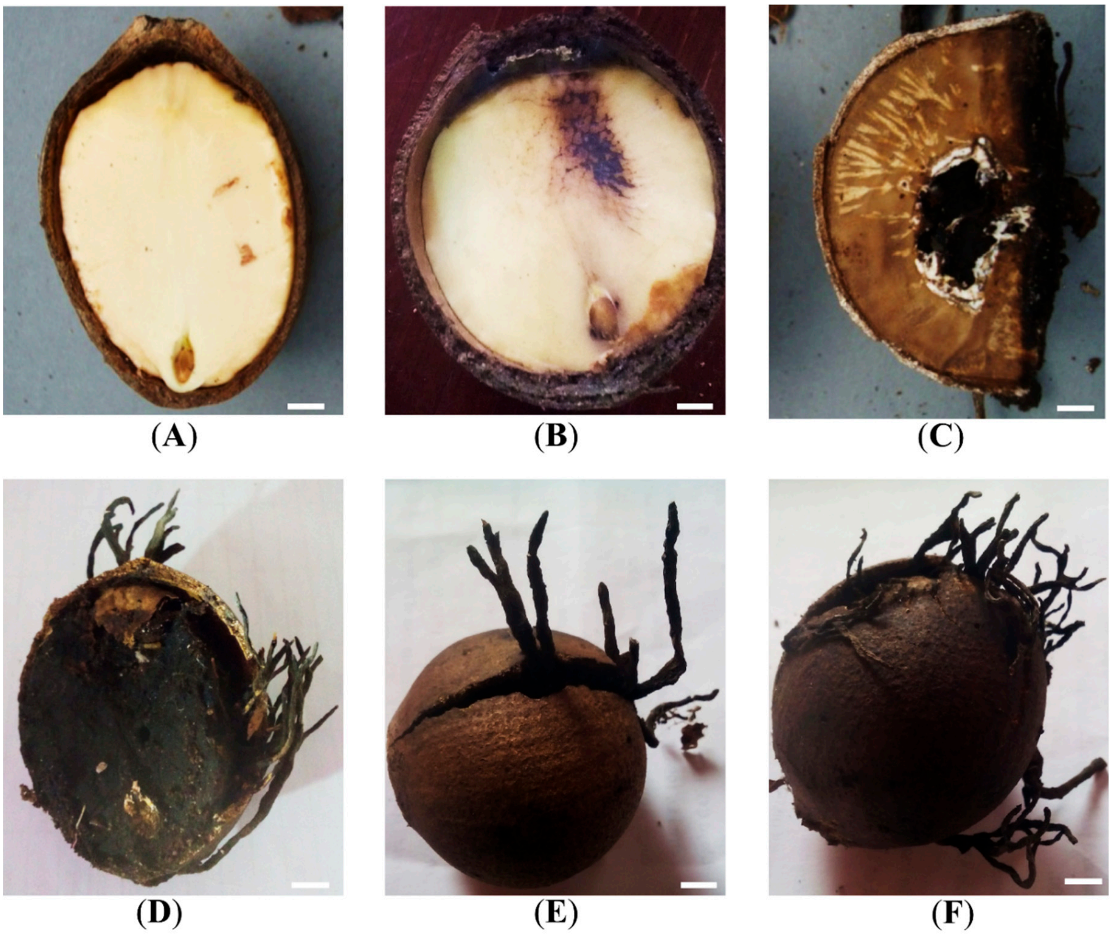

Figure 1. Symptoms of *Xylaria karyophthora* on *Chlorocardium* spp. (Lauraceae) seeds from Guyana. (**A**) Healthy seed; (**B**,**C**) Early stages of infection; (**D**–**F**) Stromata of *Xylaria* on Greenheart seeds. Bar = 10 mm.

6. Mycofloristic Studies of Xylariaceous Fungi from the Neotropics

Xylaria Hill ex Schrank is the largest and most well-known member of the Xylariaceae [43]. This genus is cosmopolitan throughout the world; however, the highest diversity is known from tropical regions [44]. Species of *Xylaria* are generally characterized by black, carbonaceous, multi-peritheciate fruiting bodies, and are generally referred to as carbon fungi. However, they can also vary from this convention (Figure 2). They play important ecological roles and are generally recognized as saprotrophic on wood and plant debris. However, they have been reported from dung and termite nests [45,46], fruits, seeds, petioles, and leaves [46], as phytopathogens [47] and as endophytes of many woody and grass species [46–48] and orchids [49].

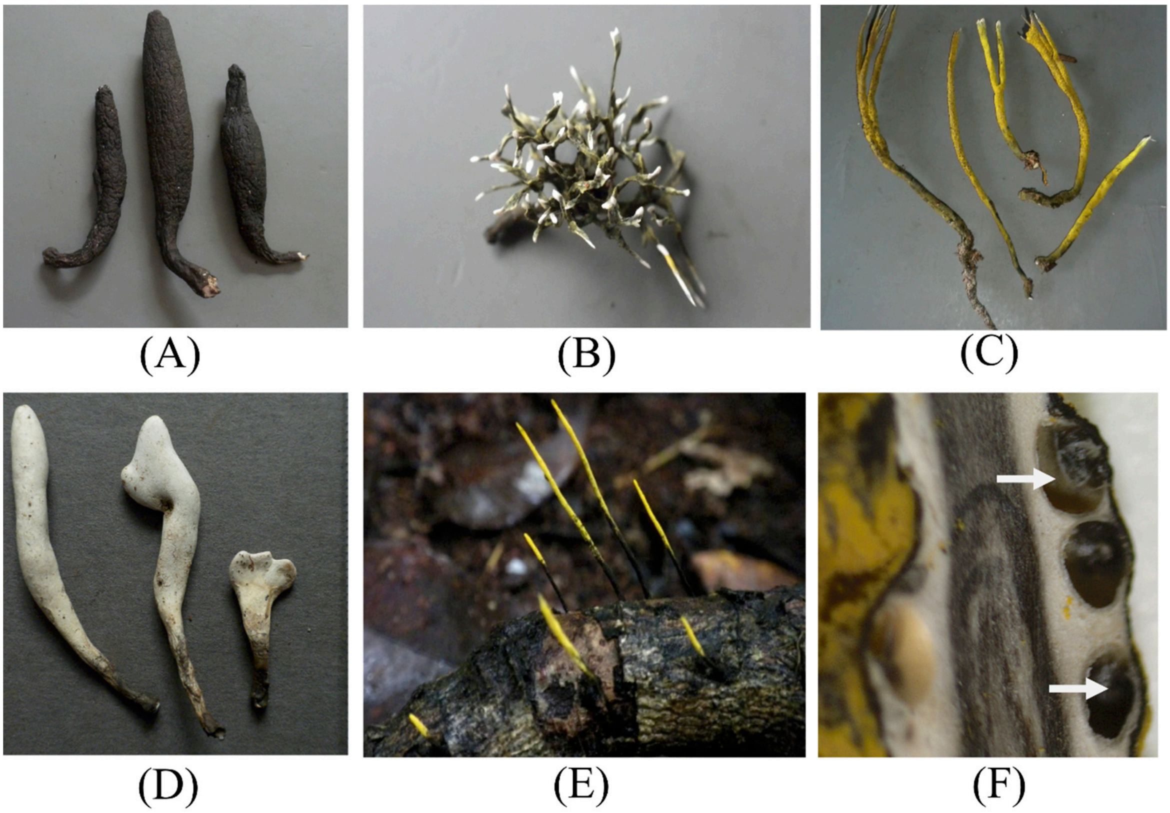

Figure 2. Teleomorphic stromata of various *Xylaria* species in Guyana. (**A**) Common black carbonaceous morphology of *Xylaria* sp.; (**B**–**E**) Other morphologically distinct forms of *Xylaria*; (**F**) Section through stromata exposing perithecia (arrows).

Even though tropical forests are vastly underexplored for fungi [50], there are numerous records of xylariaceous species from Neotropical regions. Pioneering studies show the documentation of numerous collections from Brazil, Venezuela, the Guianas, Suriname, and the Caribbean [51]. The works of Spegazzini [52–54] added several collections from Argentina, Bolivia, and Venezuela. Theissen [55], Rick [56], and Duarte and Ferreira [57] also contributed significantly to known *Xylaria* species from Brazil. Early published work by Rogers and Callan [58] also provide evidence of *Xylaria* from Venezuela, while more recent investigations by San Martin and Rogers [59] offer extensive records of wood-rotting *Xylaria* species from Mexico in various forest types on various substrata. Records show documented collections from Belize, Ecuador, and the Guianas by Læssøe [60] and more recently in Brazil [61,62]. As part of a study on Neotropical macromycetes from montane and cloud forests, Lodge and colleagues [41] documented 13 species of *Xylaria* from the upper Potaro River basin in Guyana. All of the identified species are saprotrophic on wood and plant debris with the exception of *X. ianthinovelutina* (Mont.) Mont., which was recorded from pods of the leguminous genus *Dicymbe*

Spruce ex Benth. *Xylaria ianthinovelutina*, however, is not a known cause of seed mortality for *Dicymbe* but is likely a specialized decomposer of the woody debris.

A culture-based study published by Cannon and Simmons in 2002 [63] on diversity and host preference of leaf endophytic fungi in the Iwokrama Forest Reserve, Guyana, found members of Xylariaceae were among the most frequently isolated from 12 tree species. At that time, the authors also made note of a xylariaceous fungus on the fruits of Greenheart, which they identified as a *Nodulisporium* species. This record is, to our knowledge, the first record of a xylariaceous fungus on Greenheart seeds, and may represent *X. karyophthora* [11].

7. Discussion

Prince [64] estimated between 150–218 years for rotation of Greenheart up to 50 cm diameter. *Xylaria karyophthora*, a fungal colonist of the seeds of both species of *Chlorocardium*, could represent a significant new and emerging threat to the forestry industry in Guyana. The long-term survivability of this important timber species could be threatened by the negative impacts of this fungus on germination and seedling recruitment. Therefore, the activities of this fungus can have far-reaching consequences for the future of Greenheart and, by extension, the forestry industry in Guyana.

A careful review of key silvicultural and mycofloristic records from Guyana revealed no evidence of a seed pathogen as a limiting factor to seedling recruitment and regeneration of Greenheart. Even though the exact time of emergence of *X. karyophthora* is unclear, a timeline of the historical records seems to indicate that this fungus emerged sometime before 2000. The almost sudden emergence of this fungus is consistent with several plausible explanations including that of a novel species introduced from a different geographic location or an endemic that became parasitic as a result of anthropogenic disturbance/changes in habitat and climate [65–67]. Further, we conducted multilocus phylogenetic analysis based on PRB2 and α-actin and found *X. karyophthora* to be derived from within a clade of wood-inhabiting species [11], suggesting a possible shift from woody to seed substrata. We therefore surmise two plausible hypotheses for the ecology of this fungus. First, is the foraging ascomycete strategy, which theorizes that saprotrophic fungi can exist as non-symptomatic micro-thalli in healthy plant tissue as a means for dispersing across challenging environments [68]. However, in this scenario, *X. karyophthora* possess the ability to move beyond the endophytic state to utilize another substrate, i.e., the seed of Greenheart, an expanded concept referred to as viaphytism [69]. Second, *X. karyophthora* could represent an emerging infectious organism due to a new host–pathogen interaction that resulted from a recent host jump to Greenheart from another unidentified host or introduced from a different geographic region [65]. From all indications, the preliminary distribution of *X. karyophthora* also shows a highly effective seed parasite passing a series of filters that correspond to successful invasion, i.e., transport, establishment, and spread [11]. Another fascinating observation is that Greenheart is found mainly in mixed stands or forming reefs (clumps) [28], however, *X. karyophthora* has only been observed in association with Greenheart seeds and not the seeds of other species in the stand. According to Rogers et al. [70] and Han and Shin [71], fruit- and seed-inhabiting *Xylaria* species are generally reported as host-specific, supporting this observation.

Accoding to Parker and Gilbert [66], emerging infectious diseases have two hypothetical causes: (1) invasive fungi are usually introduced and result from new host–pathogen interactions (e.g., host jump between related or unrelated taxa); (2) new infectious organisms can arise resulting from hybridization of novel co-occurring allopatric species. There are numerous examples in the literature of deadly epidemics cause by introduced/invasive agents [72,73]. Their negative influence on native species, communities, and ecosystems has been well documented for decades [66]. Any efforts to limit their damage would require an understanding of their current and potential distribution, factors affecting their spread, their ecology, and the establishment of appropriate management strategies. In the case of *X. karyophthora*, additional analysis using molecular tools to determine geographic origin and dispersal biology is also necessary. Another parameter to consider is the fact that Guyana's forests house considerable macro-fungal diversity but the total diversity of the resident macromycetes are largely unknown [74]. The situation is further exacerbated by the cryptic nature of these fungi limiting chance encounters during any expeditionary effort [50]. These circumstances therefore present considerable limitations to quickly recognizing the difference between native and introduced species as well as early detection of novel phytopathogens and highlights the importance of baseline data for understanding and combating any newly emergent disease.

8. Conclusions

Xylaria karyophthora is the first report of a *Xylaria* spp. associated with the fruits of a *Chlorocardium* species and possibly the first non-endophytic *Xylaria* associated with the seeds of any member of the Lauraceae. It is evident from the historical record that this fungus was not reported before the 2000s and represents a foreseeable threat with the power to change the landscape of Greenheart and, by extension, the forestry industry in Guyana. It is evident from the literature that much of what we know regarding fruit- and seed-inhabiting *Xylaria* species is limited to their taxonomy. Rogers [75] raised the question as to whether fruit-inhabiting *Xylaria* species infect their host during fruit development by way of the flowers. Answers to questions relating to structure and epidemiological potential are poorly documented. Further, the influence of anthropogenic disturbance and climate change on the activities of these fungi are also either sparse or non-existent. These data will be necessary for understanding the impact that *X. karyophthora* may pose for the Guyanese Greenheart industry.

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