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2	Local Neighbourhood Affects the Crowns and Root Systems of Five
3	Tropical Tree Species
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13 14	A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Biology
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Abstract

80	Biodiversity-Ecosystem Function (BEF) research in forests lacks a solid foundation of
81	below-ground studies that consider coarse roots, and documented analyses that include both
82	crown and root system are sparser still. This thesis seeks to fill this knowledge gap by assessing
83	the influence of the tree neighbourhood (e.g. size and species identity of neighbouring trees) and
84	abiotic characteristics (e.g. soil nitrogen content, depth to water table), first on coarse root traits
85	such as length, diameter and number of coarse lateral roots, and second on the extent and shape
86	of crowns and root systems. We used mixtures of tree species (monoculture, two- or three-, and
87	five-species mixtures) planted in 2001 at the Sardinilla experiment in Panamá.
88	In 2017, 128 trees of 13.27 ± 4.73 m mean height were destructively harvested above-
89	ground, and their root systems up to 0.5m radius and 0.2 m depth from the stem were excavated
90	from the soil to expose the core of their root systems. In addition, a primary lateral root was
91	chosen randomly and fully excavated; species-specific allometries were used to predict the
92	length of all unexcavated primary roots. Terrestrial laser scans taken in 2017 were used to
93	calculate the 128 trees' two-dimensional crown shapes. With these data, seven root traits were
94	described, including four observed (primary root number, diameter and length, and number of
95	secondary roots per meter of primary root) and 3 predicted traits (root system extent, total length
96	of roots per focal tree, and coarse root biomass), as well as crown and root system area and an
97	index of compactness of these systems. Focal tree biomass was plotted against the Hegyi
98	distance-dependent competition index at three distinct neighbourhood extents (nearest
99	neighbours, above- and below-ground neighbours) to identify the neighbourhood scale that best
100	explained focal tree growth. Canonical correspondence analysis was used to identify which

aspects of neighbourhood composition and environmental characteristics explained a majority ofvariation in the tested root and crown traits.

103 Larger trees tended to have more extensive and numerous primary roots, and the 128 104 focal trees' root systems were on average 2.6 ± 1.1 (standard deviation) times wider than their crowns. The size and species identity of near neighbours explained more variation than 105 106 environmental characteristics: compare 63.0% versus 30.4% variation in the seven coarse root 107 traits explained, and 65.8% versus 26.0% variation explained in crown and root extent and morphological traits. The nearest neighbourhood best predicted focal tree biomass (\mathbb{R}^2 of 0.46), 108 109 suggesting the paramount importance of competition with near neighbours for the biomass and above- and below-ground architecture of two-decade-old tropical trees. However, certain trends 110 in root architecture were observed in response to biotic and abiotic variables: trees growing with 111 conspecific neighbours, in nitrogen-rich plots or in soil with a lower mean water table height 112 tended to have more and shorter primary roots. These findings further our understanding of how 113 114 tropical tree roots and crowns respond to their local biotic and abiotic environments, plastically altering architecture and morphology to better cope with competing neighbours and nutrient or 115 116 water supply.

117

Résumé

119	La recherche sur la biodiversité et les fonctions des écosystèmes (BEF, en anglais) dans
120	les forêts manque encore d'études qui prenant en compte les grosses racines, ainsi que d'analyses
121	documentées considèrant la couronne et le système racinaire. Par conséquent, cette thèse étudie
122	l'influence du voisinage des arbres (par ex. la taille et l'identité des espèces des arbres voisins) et
123	des caractéristiques abiotiques (par ex. la concentration d'azote du sol ou le niveau
124	piézométrique), même pour les traits racinaires tels que la longueur, diamètre et nombre de
125	racines latérales primaires, comme pour l'étendue et la forme des couronnes et des systèmes
126	racinaires. Nous avons utilisé des parcelles d'arbres (monoculture, mélanges de deux, trois ou
127	cinq espèces) plantés en 2001 à Sardinilla, en Panamá.
128	En 2017, 128 d'arbres ont été exploités de manière destructive et dans un rayon de 0,5
129	m et d'une hauteur de 0,2 m ont été extraits du sol pour exposer le noyau du système racinaire.
130	De plus, une racine latérale primaire a été choisie au hasard et entièrement excavée; des
131	allométries spécifiques aux espèces ont été utilisées pour prédire la longueur de toutes les racines
132	primaires non excavées. Les balayages laser terrestres effectués en 2017 ont été utilisés pour
133	calculer les formes de cimes bidimensionnelles des 128 arbres. Avec ces données, sept traits
134	racinaires ont été décrits, dont quatre observés (le nombre, diamètre et longueur des racines
135	primaires, et le nombre de racines secondaires par mètre de racine primaire) et trois traits prédits
136	(l'étendue du système racinaire, la longueur totale des racines, et la biomasse racinaire
137	primaires), ainsi que de la couronne et du système racinaire et un indice de compacité de ces
138	systèmes. La biomasse des arbres focaux a été comparée à l'indice de compétition de Hegyi en
139	fonction de trois étendues de voisinage distinctes (les voisins les plus proches, les voisins au-
140	dessus et au-dessous du sol) pour identifier l'échelle spatiale qui explique le mieux la croissance

des arbres focaux. Une 'analyse de correspondance cononique a été utilisée pour identifier les
aspects de la composition spatiale et des caractéristiques environnementales expliquant la
majorité de la variation des caractères de racine et de couronne testés.

Les grands arbres ont tendance à avoir des racines primaires plus étendues et plus 144 nombreuses que les petits, et le système racinaire de les 128 arbres exploitées est en moyenne 2,6 145 \pm 1,1 (l'écart type) plus large que leur cime. La taille et l'identité de l'espèce des voisins proches 146 expliquent plus la variation que les caractéristiques environnementales: 63,0% contre 30,4% de 147 148 la variation des sept caractères des grosses racines expliqués, et 65,8% contre 26,0% variation expliqué pour l'étendue de la couronne et des racines et les traits morphologiques. La biomasse 149 des arbres focaux a été mieux prédite par le voisinage le plus proche (\mathbb{R}^2 de 0,46), ce qui suggère 150 que la compétition avec des voisins proches détermine la biomasse d'arbre ainsi que 151 152 l'architecture aérienne et souterraine. Cependant, certaines réponses de l'architecture racinaire ont été observées en réponse à des variables biotiques et abiotiques: les arbres poussant avec des 153 154 voisins conspécifiques, dans des parcelles riches en azote ou dans un sol où le niveau 155 piézométrique était plus bas, avaient des racines primaires plus nombreuses et plus courtes. Ces 156 résultats permettent de mieux comprendre comment les racines et les couronnes des arbres tropicaux réagissent à leurs environnements biotiques et abiotiques en modifiant l'architecture et 157 la morphologie de manière plastique afin de mieux atteindre de la lumière, les nutriments ou 158 l'eau en sol en compétition avec des voisins. 159

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Preface

220 **Thesis Format and Style**

221 This Masters thesis comprises two manuscripts intended for publication in scientific 222 journals. The first chapter takes variation in coarse root traits as its focus by exploring and comparing the effect(s) of tree neighbourhood composition and abiotic variables (including 223 224 edaphic, hydrologic and topographic characteristics) on the morphology and extent of single, 225 excavated roots and of entire root systems. The second chapter extends this analysis of how tree 226 traits are influenced by the local environments in which trees grow, including in its scope both 227 crown and root system area and compactness (an index that quantifies the crown or root system's non-symmetric growth around the focal tree). Both chapters utilize data of five tropical tree 228 229 species grown in the Sardinilla planted forest in Panama.

231 **Contributions of Co-Authors**

Chapter 1: My supervisor, Dr. Catherine Potvin, was one of the co-founders of the 232 Sardinilla Biodiversity Experiment (http://www.treedivnet.ugent.be/ExpSardinilla.html). In 233 234 addition, Catherine developed the field methodology used to excavate the roots, supervised the 235 root excavation and tree harvesting field work, and provided access to yearly tree census data 236 from Sardinilla. Dr. Jefferson Hall and Dr. Katherine Sinacore shared their root system dataset 237 with us, enabling me to validate the methodology I used to predict the length of unexcavated roots and also to compare our findings with theirs, producing a simple time-series analysis. As 238 239 comparable root data is notably rare, especially in tropical systems, having access to their dataset was a great boon to me. Florian Schnabel, a German colleague who is a member of the 240 TreeDivNet group of scholars, generously provided me with numerous competition indices he 241 had calculated for the Sardinilla site. 242

Chapter 2: Dr. Potvin was again instrumental in the provision of data and editing of the numerous drafts of this paper. The data of Drs. Hall and Sinacore were again used in this chapter, enabling us to perform a comparison of root:shoot ratio of three tropical tree species through time. The aspects of this chapter that related to crown morphology and terrestrial laser scanning (TLS) were introduced to me by Dr. Matthias Kunz and Professor Goddert von Oheimb, who also taught me the fundamentals of how to work with this kind of data and supplied me with TLS data for the focal trees used in this study.

I contributed to both chapters of this thesis. Under the guidance of Dr. Tim Moore
(McGill Professor in the department of Geography), I carried out soil sampling and some
analytical laboratory work on the soil samples. I spent many months cleaning and analyzing root

- and whole-tree data. With much help from Catherine, I was the principal author for both
- 254 manuscripts that make up this thesis, and I also wrote this thesis.

Acknowledgments

« Nous sommes comme des nains assis sur des épaules de géants. Si nous voyons plus de
choses et plus lointaines qu'eux, ce n'est pas à cause de la perspicacité de notre vue, ni de notre
grandeur, c'est parce que nous sommes élevés par eux. »

259

-Bernard de Chartres, according to Jean de Salisbury

260 The metaphor of the 'dwarf on the shoulders of a giant' applies well to this thesis, which benefited immeasurably from nearly two decades of work of my supervisor Dr. Catherine Potvin 261 and her colleagues in the Sardinilla and TreeDivNet scholar groups. My supervisor, Dr. 262 Catherine Potvin, has been an invaluable source of inspiration, motivation, course-correction and 263 wisdom. She contributed much of her time to help me conceptually form and edit both chapters 264 of my thesis. I greatly appreciate her taking me on as a graduate student and her invitation to be a 265 266 part of this research group's legacy. Graduate school can be a challenging time as one is faced with new challenges and opportunities to learn; friends and colleagues in the BESS 267 (Biodiversity, Ecosystem Services and Sustainability) programme at McGill were supportive 268 companions who shared much of their knowledge with me. My fiancé Kamila Araujo also saw 269 270 me through the ups and downs of this process, providing me with endless support. 271 I am extremely grateful to the team of field technicians and scientists that carried out the

271 Tam extremely graterul to the team of field technicians and scientists that carried out the
272 grueling task of unearthing some two-hundred root systems over months of hard work; Dr.
273 Potvin, German colleague Florian Schnabel, and many Panamanians made up this team, and to
274 all of them I say "¡muchas gracias!" Dr. Tim Moore was a mentor to me in soil field analyses,
275 and the generosity and supervision of Dr. Ben Turner and his colleagues and staff at the

276 Smithsonian Tropical Research Institute enabled me to perform soil analyses that otherwise277 would have been impossible!

Many knowledgeable individuals generously advised me on how to tackle the numerous analyses used in this thesis; I particularly want to extend a hearty thanks to Ms. Mélanie Desrochers and Mr. Daniel Lesieur, who took me under their proverbial wings to teach me the basics and respond to my many e-mails concerning GIS and Microsoft Access. Fellow BESS student Marc-Olivier Beausoleil was a very supportive mentor for me in learning R, his love of which has infected me.

I must thank the scholars of the TreeDivNet and, particularly, the Sardinilla group, for their feedback regarding the two chapters of my thesis. Each member of these groups commands an impressive knowledge of forest ecology and are masterful in their ability to communicate their science with the written word.

288 Financial Support

I owe thanks to funding from many sources: Dr. Potvin supported me generously from 289 her own Research Chair funding; the BESS programme supplied me with funds for my stipend 290 291 as well as travelling and carrying out field research; the Biology Department of McGill supported me through funding travel, field work, soil chemical analyses, and more; the Centre 292 d'Étude de la Forêt and the FRQNT (Fonds de Recherche Nature et Technologies Quebec) 293 granted me funds that enabled me to carry out field work and carry out an unforgettable 294 internship in the deep jungles of Panama. I am deeply grateful to Mr. Luc Lauzon for his help in 295 296 securing this last source of funding.

297

General Introduction and Literature Review

299

300 Forests are an important for life on earth because they interact with global and local 301 environmental cycles (carbon, water, others) and they form the basis of many terrestrial ecosystems. Their importance for humans has been itemized as a list of the ecosystem services 302 they provide (García-Nieto et al., 2013; Biber et al., 2015; Joshi & Negi, 2011). Perhaps the 303 304 service we most commonly associate with forests is the production of wood and other forest products (Chiabai et al., 2011; Uddin et al., 2013). Forests also perform many other essential 305 functions, including filtering the air and water (Bolund & Hunhammar, 1999; Joshi & Negi, 306 2011; Smith et al., 2012), maintaining terrestrial biodiversity (Mori et al., 2016; Brockerhoff et 307 al., 2017), sequestering carbon dioxide from the atmosphere and fixing it into woody matter and 308 309 soil (Bonan, 2008; Díaz et al., 2009; Comas & Eissenstat, 2009), reducing soil erosion (Dymond et al., 2011), and supporting indigenous ways of living that are more closely linked with and 310 311 dependent on forests (Berkes & Hunt, 2006; Nkem et al., 2013; Gould et al., 2014). The planting of new forests and maintenance of current stands is particularly valuable in the context of off-312 setting anthropogenic climate change through carbon sequestration (Watson et al. 2018; Bonan, 313 2008). Indeed, an assessment of potential 'natural solutions' to anthropogenic climate change 314 highlighted reforestation, the avoidance of forest clearing, and the management of natural forests 315 as the cost-effective options with the highest climate mitigation potential by 2030 (Griscom et 316 317 al., 2017).

Humankind has had a significant and largely negative impact on forests globally, decreasing the amount of forest cover by deforestation or degrading forest integrity: according to the FAO (2015), 57% of forests today were once cleared by humans and now are secondary growth. Tree

plantations have been established to serve part of the market's need for wood, which now make 321 up about 7% of forests globally (FAO, 2015). Managed forests may sequester less carbon over 322 323 the long term compared to unmanaged forests, and more carbon tends to be allocated aboveground in managed forests than in unmanaged forests (Noormets et al., 2015); however, certain 324 325 synergies may exist between complementary ecosystem services, such as between carbon 326 sequestration and biodiversity maintenance (Nelson et al., 2009; Bullock et al., 2011; Smith et al., 2012; Brockerhoff et al., 2017). Therefore, forests can be managed for the simultaneous 327 328 conservation of biodiversity and sequestration of carbon under such economically feasible 329 management strategies as 'assisted natural regeneration' (Evans et al., 2015). Indeed, Lu et al. (2018) argued that many of the monoculture planted forests in Europe have been converted to 330 species mixtures for both economic (increased productivity of wood resources) or conservation 331 (restoring or safeguarding biodiversity) purposes. 332

333 Research on the effects of biodiversity on ecosystem functioning (BEF) have revealed a 334 generally positive effect of species and functional diversity on productivity (Healy *et al.*, 2008; Morin et al., 2011; Ruiz-Benito et al., 2013), resilience to invasive species and disturbances 335 (Tilman & Downing, 1994), and resource use efficiency (Tilman, Wedin and Knops, 1996; Lei et 336 337 al., 2012). Experimental research has been dominated by planted grasslands (e.g. Xu et al., 2018) due to quick responses to treatments and fairly easy manipulation (Brassard et al., 2012). BEF 338 339 experiments in forests has received less attention (Morin et al., 2011), thus the establishment of long-term planted forests that explore how species and functional diversity affect ecosystem 340 341 functioning is helping to close this knowledge gap (e.g. TreeDivNet sites, Verheyen et al., 2016). Forests are composed of woody, perennial individuals of a much larger scale than grasses, 342 enabling the study of their architectural response to external stimuli over time (Longuetaud *et al.*, 343

2013; Jucker *et al.*, 2015, Guillemot *et al.*, in review), while their large size means that we can
conceptualize and measure the competitive and/or facilitative interactions between individuals
(Clark, 2010; Juchheim *et al.*, 2017). Forest stands composed of multiple species can exhibit
greater productivity than monocultures due to competitive reduction or facilitation between
functionally distinct species (Fichtner *et al.*, 2017), which may result in more efficient resource
and space use (Jucker *et al.*, 2015; Forrester & Bauhaus, 2016).

Despite their undeniable importance for tree growth (Metcalfe et al., 2002), seedling 350 recruitment (Gunaratne et al., 2011), and competition for water and soil nutrients (Coomes & 351 352 Grubb, 2000; Rewald & Leuschner, 2009), tree roots have garnered less attention and study than tree crowns (Comas & Eissenstat, 2009; Brassard et al., 2013; Lang'at et al., 2013; Sinacore et 353 al., 2013; Klingenburg & Leuschner, 2018), largely because of the great investment of time and 354 effort that root excavations require (Mao et al., 2015). This is especially the case for larger trees 355 356 and tropical trees, which may exhibit significantly different allometries between above- and 357 below-ground biomass than their younger counterparts (Kenzo et al., 2009). Therefore, this thesis seeks to fill the knowledge gap of how tropical trees respond to the constraints of their 358 359 local neighbourhood and environment by plastically altering their root and crown traits.

This thesis seeks to further our understanding of how trees interact with their neighbour and local abiotic environmental conditions in two contexts: first, it takes a close look at how trees vary their architectural root traits (e.g. root length, diameter, and intensity of root bifurcation) according to external factors such as competition with neighbours or water table depth; second, it compares the extent and compactness (a measure of symmetry in branch or root length around the central axis of the tree) of the focal trees' crowns and root systems, seeking to link the aboveand below-ground compartments of the trees through the identification of neighbourhood or

367 environmental variables that affect both tree compartments similarly. The hypotheses tested in the first chapter are as follows: that focal tree root length is reduced when the focal tree's 368 neighbours are taller than the focal tree and thus reduce available light for the focal tree, that 369 focal trees in plots of species mixtures have broader root systems than those in monocultures 370 (Brassard et al., 2013; Bu et al., 2017), and that neighbour identity and size more strongly affect 371 372 focal tree coarse root traits at Sardinilla than abiotic environmental factors (Valverde-Barrantes et al., 2013). In the second chapter was organized by three structuring objectives: to compare the 373 twenty-year old trees' crown and root system extents, to test which neighbourhood scale (nearest 374 375 neighbours, crown neighbours and root system neighbours) most accurately explains focal tree biomass, and to identify which aspects of the focal trees' local environment (e.g. competition 376 377 with neighbours, soil nitrogen or water availability, etc.) most strongly impacted focal tree crown and root extent and compactness; for this last objective, we hypothesized that neighbourhood 378 characteristics would explain more of the variation in these crown and root system variables than 379 380 edaphic, hydrologic or topographic variables.

382	Coarse Root Architecture: Neighbourhood and Abiotic
383	Environmental Effects on Five Tropical Tree Species Growing in
384	Mixtures and Monocultures
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406 Abstract

407 Most biodiversity-ecosystem function research focusses above-ground; if it considers roots, it considers fine roots, while coarse roots remain a "black box". We utilized the Sardinilla 408 409 experiment in Panamá, the oldest tropical tree diversity experiment, to test how species mixtures 410 at the plot and neighbourhood scales and abiotic environmental characteristics affected 7 coarse root traits of 5 tropical tree species. Sardinilla was planted in 2001 with a gradient of native tree 411 412 species richness of two-, three- and five-species mixtures and their respective monocultures. 413 Root systems of 128 mature trees were excavated 0.5 m radially and one coarse root was fully 414 excavated; unexcavated root lengths were predicted using species-specific allometric relationships. Root traits included the observed traits primary root length, diameter, and number, 415 416 the number of secondary roots per meter of primary root, predicted root system extent and total 417 predicted length of roots, and coarse root biomass. Tree size scaled positively with most root 418 traits. Species identity (conspecific or heterospecific) and size of near neighbours were found to 419 explain more variation (63.0%) in root traits than abiotic environmental characteristics (30.4%). Trees in waterlogged plots grew fewer, longer roots. Trees reduced root system extent but grew 420 421 more roots when growing with conspecifics or growing in plots of high soil nitrogen and greater 422 depth to water table. These findings suggest strategies employed by tropical tree species to both 423 reduce competition with neighbours and make the most of local abiotic conditions, bringing us 424 closer to understanding the role of coarse roots in the context of BEF research in forests.

425

426 Introduction

427 In the last two decades, numerous studies have demonstrated increased productivity in species mixtures compared to monocultures in both natural (Brassard et al., 2013; Prado-Junior 428 429 et al., 2016; Baeten et al., 2019) and planted forests (Potvin & Gotelli, 2008; Cunningham et al., 430 2015; Mayoral et al., 2017; Schnabel et al. 2019; Huang et al., 2018). This phenomenon has been observed in temperate (Baribault & Kobe, 2011; Forrester & Albrecht, 2014) as well as in 431 432 tropical forest sites (Potvin & Gotelli, 2008; le Maire et al., 2013; Sapijanskas et al., 2014; Huang et al., 2018; Schnabel et al. 2019). Asking questions regarding mixture effects in forests 433 434 demands focussing at the level of individual trees, the growth and mortality of which determine productivity at the plot/stand level (Potvin & Gotelli, 2008). Trees are influenced by near 435 neighbours directly via such mechanisms as competition for light (Potvin & Dutilleul, 2009; von 436 437 Oheimb et al., 2011; Aakala et al., 2013; Schnabel et al, 2019), litter production and below-438 ground interactions (Sapijanskas et al., 2013). Tree species identity has been shown to 439 significantly affect the competition or facilitation that occurs between trees in potted plant 440 experiments (Belter & Cahill, 2015), planted forests (Uriarte et al., 2010; Setiawan et al., 2016; 441 O'Brien et al., 2017; Chen et al., 2018), and mature forests (Valverde-Barrantes et al., 2013). 442 Depending on their life history, species may engage in stronger competition with conspecific neighbours than with heterospecific neighbours, be unaffected by the identity of neighbours, or 443 compete less with conspecific neighbours (Uriarte et al., 2004). However, in general, growth 444 rates of focal trees have been shown to be higher when growing with heterospecific neighbours, 445 446 such as in mature tropical forests in Malaysia (Stoll & Newbery, 2005), China (Liu et al., 2016) and in Panamá (Chen et al., 2018). Similarly, focal tree growth was found to increase with 447 neighbourhood species richness in planted tree diversity experiments (Fichtner et al. 2018, 448

Schnabel *et al.* 2019). However, Setiawan *et al.* (2014) used young planted forest plots
established in 2010 in Belgium to provide evidence that only certain combinations of species
manifest positive mixture effects.

452 Much of the literature of tree-tree interactions focusses on above-ground metrics such as 453 annual basal diameter growth in response to neighbourhood diversity or competition through 454 shading (e.g. Forrester & Albrecht, 2014; MacFarlane & Kane, 2017; Van de Peer et al., 2017, Schnabel et al., 2019), because below-ground measurements are relatively difficult to take. 455 456 However, the positive BEF relationships commonly observed in forests may be in part due to 457 plasticity in root traits in response to species diversity, identity, and interactions with neighbours (Sapijanskas et al., 2014; Mina et al., 2018). Indeed, a recent review of mechanisms underlying 458 459 diversity-productivity relationships in forests suggested that more efficient water or soil nutrient absorption below-ground is vital for above-ground biomass allocation (Ammer, 2019). The 460 461 responsiveness of roots to the presence of neighbours has been documented by authors such as 462 Cahill & McNickle (2011), whose greenhouse experiments illustrated that roots can react to the presence of other roots with either no response, avoidance (directional change of growth at root 463 464 apical meristem), or aggregation (increased root tissue investment by the plant to outcompete its 465 neighbour(s)), depending on the neighbour's identity and how the focal species reacts to con- or hetero-specific neighbours. Herbaceous plants have indeed been shown to be able to differentiate 466 467 between their own roots and those of neighbours (Gruntman & Novoplansky, 2004; Karban & Shiojiri, 2009), as well as between con- and hetero-specific neighbour roots (Dudley & File, 468 469 2007; Murphy & Dudley, 2009). Studies of herbaceous plants growing in the presence of neighbours have yielded mixed results (Faget et al., 2013). When growing with conspecific 470 neighbours, Impatiens pallida (Murphy & Dudley, 2009) invested less in root systems, as did 471

Cakile edentula var. lacustris when growing with more closely related conspecifics (Dudley & 472 473 File, 2007). Conversely, soybean plants (*Glycine max*) grown together in pots were shown to 474 allocate more resources to below-ground growth than others grown in their own pots (Gersani et al., 2001). Contrary to this result, Jacob et al. (2017) found that the ratio of root: shoot allocation 475 in pea plants (*Pisum sativum* L.) wasn't significantly affected by neighbour identity, but rather 476 477 by neighbour presence. Proposed mechanisms for such differentiation include soluble chemical signals released into the soil (Biedrzycki et al., 2010), growth-inhibiting chemicals released into 478 479 the soil and physical contact between roots (Mahall & Callaway, 1992). Biedrzycki et al. (2010) 480 provided experimental evidence of such chemically induced growth inhibition in Arabidopsis thaliana plants grown in the presence of kin and non-kin plants. 481

In her review of general plant root growth and plasticity, Hodge (2009) described how 482 plants also vary their root placement to maximize nutrient absorption in response to various cues 483 such as local soil nutrient concentrations. Therefore, different species may respond to a given 484 485 combination of environmental and neighbourhood cues with distinct root placement and proliferation strategies (Kembel & Cahill, 2005). Croft et al. (2012) proposed a fixed hierarchy 486 of cues wherein soil resource availability is the most important factor, followed by interactions 487 488 with neighbours, while symbiotic relations with mycorrhizae are the least important. The avoidance strategy has also been described as "size-sensitivity" by Belter and Cahill (2015), who 489 490 posited that plants may also exhibit so-called "location-sensitivity," wherein they exhibit more 491 space-efficient use of soil through vertical or horizontal stratification of roots.

The bulk of the work that has been done on below-ground Biodiversity-Ecosystem Functioning (BEF) effects in forests has focussed on the fine roots of trees, as they represent important organs for nutrient and water absorption and soil structural integrity (Jones *et al.*,

2011; Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016). Tree species richness has been shown
to increase both fine root productivity at multiple soil depths (Brassard *et al.*, 2013) and specific
root length of fine roots (Bu *et al.*, 2017) in temperate deciduous forests. Weemstra *et al.*'s metaanalysis (2016) found that fine roots respond to numerous constraints on growth which results in
a multidimensional spectrum that encompasses nutrient absorption, symbiosis with mycorrhizae,
and competition with other roots (Bardgett *et al.*, 2014; Kramer-Walter *et al.*, 2016; Bergmann *et al.*, 2017).

502 While fine roots play a key role in nutrient absorption, coarse roots are important for various functions including carbon storage (Wang et al., 2012), soil exploration (i.e. lateral 503 expansion) and anchorage (Sorgonà et al., 2018). To increase our understanding of diversity-504 productivity relationships below-ground, we used the Sardinilla planted forest in Panamá to 505 explore how tree species mixtures at plot and neighbourhood scales and environmental factors 506 affected coarse root growth patterns of five tropical tree species. The specific root length of 507 508 coarse roots (Valverde-Barrantes et al., 2013) and ratios of coarse root:crown biomass (Bolte et al., 2004) in temperate deciduous forests have been shown to increase with tree species richness. 509 Haggar and Ewel (1997) performed a pioneering study of how the plot-level biomass varied 510 511 between monoculture plots (trees only) and plots in which one tree species was interplanted with understorey monocots (*Euterpe oleraceae*, a palm, and *Heliconia imbricata*, of Heliconiaceae). 512 513 Their results showed that the tree species reacted distinctly to the presence of monocot 514 neighbours, and that plot-level productivity increased only in plots where the tree species did not 515 monopolize above- and below-ground resources. In contrast with Haggar and Ewel's (1997) 516 study design, in which tree species were not planted together in plots but rather in monocultures, 517 in our 17-year old Sardinilla site each tree species was planted in monoculture and in mixtures of

three- and six trees species. This allowed for comparisons of species performance in various 518 species assemblages. We use four observed and three predicted root traits to describe root 519 520 systems: observed traits include the length of excavated roots (LERoot), the specific root length (SRL), the number of primary roots, and the number of secondary roots per meter of primary 521 root; the predicted root traits are the mean effective radius of the root system, the total length of 522 523 coarse primary roots and the estimated coarse root biomass. We tested three hypotheses: (1) Shading by tall neighbours decreases focal tree root length and root system extent; 524 (2) Tropical trees in mixed stands have more extensive roots and root systems than in 525 monocultures (Brassard et al., 2013; Bu et al., 2017); 526 (3) At the examined tropical site, neighbourhood characteristics play a greater role in 527 determining root system traits than abiotic conditions (Valverde-Barrantes et al., 2013). 528 529

530 Materials and Methods

531 *2.1 Study Site*

The planted tree diversity experiment was established in Sardinilla, Panamá (9°19' N, 532 533 79°38' W), in 2001. Six native tree species, Anacardium excelsum (AE), Cedrela odorata (CO), 534 Cordia alliodora (CA), Hura crepitans (HC), Luehea seemanii (LS) and Tabebuia rosea (TR), 535 were planted in two monoculture plots each and allocated to mixtures based on their relative 536 growth rates in nearby natural forests (Scherer-Lorenzen et al., 2007). LS and CA are the 537 quickest growing species, AE and HC are intermediate, and CO and TR grow the slowest. In 538 each of the six plots of 3-species mixtures, two conditions were met: one representative of each growth-rate group was present, and each species was present in three of the 3-species mixture 539 plots (Scherer-Lorenzen et al., 2007). Mean annual temperature at the site is 25° C with an 540

average annual precipitation of 240 cm, 25 to 50 mm of which falls in the dry season while 5 to 541 10 times that falls in the wet season between May and November (Scherer-Lorenzen et al., 542 2007). Local soil is principally Tertiary limestone with a high clay content and marked 543 differences in moisture between high and low precipitation seasons; they have been described as 544 Cambisols or Tropudalfs (Soil Survey Staff 1990, Moore et al., 2018). Originally, 24 mixture 545 plots of approximately 2025 m² each were established, including: 6 six-species, 6 three-species, 546 and 12 monoculture plots. Individuals were planted according to a multiple Latin-square design 547 548 such that, in three-species mixtures, each species was surrounded by the same neighbour species, 549 as described in Potvin and Dutilleul (2009, see their Figure 1). Because of high mortality of CA, its two monoculture plots were discontinued (Scherer-Lorenzen et al. 2007), resulting in realized 550 mixture levels of 2-, 3- and 5-species mixtures; 2- and 3-species mixtures were considered one 551 treatment level, hereafter called '3 species mixtures', to preserve a balance in sample sizes 552 between mixture treatments. 553

554 2.2 Root System Measurements and Biomass Estimation

Sixteen years after planting, an intensive data collection campaign was conducted in 555 556 which 232 trees were selected from the site's 3271 live trees to be harvested using stratified random sampling controlling for size classes (small, medium and large). The root systems of 128 557 of these trees, representing all 3 size-class categories, were excavated in a 50-cm radius circle 558 559 centred on the bole to a depth of about 20 cm. The number of roots and their diameter at 50-cm from the tree trunk were also measured. One coarse root per tree was randomly selected by the 560 field workers from among the lateral roots arising from the root crown and was excavated to its 561 end, vielding individual root length data; in addition, all secondary roots' initial diameters were 562 measured. We also recorded data including each excavated root's diameter at two-meter intervals 563

and the path of the root's growth. The fresh weights of the middle and distal 2-meter root pieces
were recorded in the field. Fine roots were not excavated due to highly clayey soil.

The shortest perpendicular distance from the end of the root to each neighbour tree was measured, enabling a spatial reconstruction of each excavated root's path of growth. We mapped the excavated roots in ArcMap (v.10.5.1). To make root length estimates and predictions more conservative, we measured the distance from each focal tree's center to the point of the excavated root furthest from the tree, along its excavated root, defining this distance the 'effective root length' (Figure 1).

To estimate coarse root biomass (CRB), root volume was first estimated for each 2-meter 572 segment of the fully excavated roots (N = 128). The volumes of these cylinders were summed for 573 574 each excavated root. The natural log of total volume was regressed against the natural log of root diameter at 50cm from the trunk, yielding an adjusted R-squared value of 0.96, a strong 575 relationship between initial diameter and total root volume. This relationship was used to predict 576 the total volume of unexcavated roots (N = 1071), for which root diameter at 50cm from the 577 trunk was known. Root tissue density was calculated with root forest weight from the middle and 578 579 distal segments of each excavated root; root volume multiplied by root tissue density yielded a conservative estimate (i.e. did not include taproots) of root biomass. Finally, the mass of the root 580 crown (under tree bole, from which primary lateral roots arise), measured in the field to the 581 582 nearest 0.1 kg, which represented a large proportion of root biomass, was added to the individual tree coarse root biomass estimates. 583

584 2.3 Unexcavated Root Length Prediction

A range of statistical modelling methods was compared in terms of their suitability to 585 predict the length of unexcavated roots and root system extent by extrapolating from excavated 586 587 roots (Table S1, Supplementary Material). Partial least-squares regression (PLSR) was selected from the essayed methods because of its capacity to account for measurement error and 588 collinearity in predictor variables (Helsen et al., 2016; Haenlein & Kaplan, 2010), as well as its 589 590 suitability to predict variables with sample sizes of less than 250 (Ohsowski et al., 2016; 591 Reinartz et al., 2009; Carrascal et al., 2009). We used PLSR to first predict the length of unexcavated roots with species-specific models based on tree allometry and root diameter (Fig. 592 1). The general model is presented in Equation 1 and supplementary methods and species-593 specific model information is presented in Table S2 of Supplementary Material. 594

595

$$L_R = D_R + DBH + D_B + H \tag{Eq. 1}$$

596 Where L_R denotes the predicted root length, D_R the initial diameter of the lateral root, DBH is the diameter at breast-height of the tree, D_B is the diameter of the tree 10 centimeters 597 above ground-level, which accounts for the presence or absence of buttresses, and H is the tree 598 height. Partial least squares regression models can be judged for suitability based on the percent 599 variance in the training data set explained by the model and by the root mean square error of 600 prediction (RMSEP). The model for TR's model explained 74.5% (RMSEP of 1.91 m), LS's 601 602 model explained 43.08% (RMSEP of 2.04m), AE explained 34.65% of training set variation (RMSEP of 4.10 m), and HC's model explained only 15.41% (RMSEP of 4.11 m). The 603 predictive accuracy of this method was verified with the dataset of Sinacore et al. (2017) (for 604 605 more information, see Supplementary Material). Root length predictions were conservative, as we constrained these lengths with species-specific coefficients of root sinuosity; the resulting 606

predicted root lengths were termed the "effective root lengths." We calculated the predicted
mean effective radius of the root system (EfRadSys) by taking the mean of the excavated and
predicted roots' effective lengths for each focal tree. Furthermore, by summing the effective root
lengths, we calculated the predicted total length of root systems (TLR; see Figure 1).



- **Fig. 1** Prediction of the length of unexcavated primary lateral roots was carried out in three steps:
- 613 predicting the lengths of unexcavated roots for each species separately, measuring their
- 614 'effective lengths' (distance from cut point at 50 cm from tree bole to furthest point in root), and
- calculating the mean 'effective radius of the root system' (EfRadSys) (N = 128 trees).

616 *2.4 Statistical Analyses*

617 *2.4.1 Analysis of Covariance*

The effects of mixture treatment and species identity on root traits were tested using a nested Analysis of Covariance (ANCOVA) model modified from Potvin and Dutilleul (2009) where focal tree size was used as a covariate to account for the effect of light competition between the focal tree and its nearest above-ground neighbours (Equation 2).

622
$$X_{ijkl} = \mu + \text{Mixture}_i + \text{Species}(\text{Mixture})_{j|i} + \text{Plot}[\text{Species}(\text{Mixture})]_{k|j(i)} +$$

623
$$c \times \text{TreeSize}_{ijkl} + b \times \text{RelHeight}_{ijkl} + e_{ijkl}$$
 (2)

624 Where Mixture_i represents the number of tree species in plot mixtures (1-, 2-3, or 5species), Species(Mixture)_{ili} represents the focal tree's species identity (AE, CO, HC, LS and 625 TR) and is nested under mixture to account for the fact that different species are present in 626 627 different mixture treatments. Plot[Species(Mixture)]_{k|i(i)} captures the effect of the planting design and was treated as a random effect. The covariate "TreeSize_{iikl}" is a function derived from the 628 629 diameter at breast-height of the focal tree. For focal trees with multiple stems, the DBH function was calculated by summing the squared diameters of each stem. We added the term 630 631 "RelHeight_{ijkl}", which represents the mean height of the nearest neighbours (maximum: 8) minus 632 the focal tree height.

Four observed root traits and three predicted root traits were selected based on either their commonness in root system literature or their ability to give a detailed picture of root system morphology and extent, or both, and analysed with ANCOVA testing; the observed traits include the number of primary roots per tree, the length of excavated roots, the specific root length (SRL), and secondary root branching intensity, while the predicted traits are the effective radius of the root system, the total length of roots, and below-ground biomass (CRB). Covariates

include focal tree diameter at breast height and the mean height of nearest neighbours minus the
focal tree height. To normalize the data, natural log transformation was used on the length of
excavated roots, secondary root branching intensity, and CRB, while square root transformation
was used on SRL, the effective radius of the root system and the total length of roots.

To assess the overall relationship between the covariates (tree size and mean height of 643 644 neighbours compared to focal tree height) and root traits, we applied linear regression in R (v.3.5.3) (R Core Team, 2019). Focal trees varied greatly in terms of size (mean diameter at 645 breast height was 19.37 ± 8.39 cm), which could have a confounding effect on the root system 646 variables. Thus, least squares means were used to adjust for the covariate of focal tree size in the 647 calculations of LERoot, SRL and EfRadSys (Figure 2) using the R package "Ismeans" (v.2.27-648 62) (Lenth, 2018). Pearson Correlation tests in R were used to test for significant correlations 649 between dependent variables. Post-hoc Tukey tests were used to test for honestly significant 650 differences between group means for groups identified in the ANCOVA; the package "agricolae" 651 652 (v.1.3-1) was used (de Mendiburu, 2019).

653 2.4.2 Canonical Correspondence Analysis (CCA)

654

Two Canonical Correspondence Analyses (CCAs) were run to assess the effect(s) of neighbourhood and environmental characteristics on observed root traits. In both CCAs, the dependent matrix included root variables: observed LERoot, the diameter of the root at 50cm from the trunk (RootDiameter), the number of lateral skeletal roots, the specific root length (SRL, calculated as root length in meters divided by root mass in kg), and the number of secondary roots per meter of primary root (also called the "secondary root branching intensity).

The first CCA was based on a matrix of neighbourhood explanatory variables and the 661 second CCA used a matrix of environmental explanatory variables. The complete neighbourhood 662 663 matrix included structural diversity variables such as the standard deviation and Gini coefficient of tree diameter (expressed as basal area) and height, and the Hegyi distance-dependent 664 competition index as calculated by Schnabel et al. (2019) using 2016 and 2017 census data. The 665 666 Gini coefficient (Gini, 1912) is a size-dependent measure of inequality and is a commonly used measure of forest structural diversity (see Schnabel et al. 2017; Lexerød & Eid, 2006). The 667 668 Hegyi distance-dependent competition index (Hegyi, 1974) estimates the competition 669 experienced by a focal tree based on neighbour tree sizes and distance. Also present in the matrix were the number of conspecific and heterospecific neighbours, plot species richness, the total 670 and mean basal area of conspecific and heterospecific neighbours, and the mortality of 671 neighbours; Table S3 in Supplementary Material presents all neighbourhood variables and their 672 sources. These variables were calculated first at the near neighbourhood (maximum 8 673 674 neighbours) for each focal tree (n = 128), from which plot mean values were calculated (n = 21plots). Variables were transformed using the Hellinger transformation from the "vegan" package 675 (v.2.5-2) (Oksanen *et al.*, 2018). To select which of these variables were used in the 676 677 neighbourhood and environmental CCAs, we used the function "ordistep" for forward stepwise CCA model selection from the "vegan" package (v.2.5-2) (Oksanen et al., 2018). The final set of 678 679 neighbourhood variables included the standard deviation of tree height (cm), the number of 680 conspecific and heterospecific neighbours, and the mean size of conspecific neighbours (cm²) 681 (Table 1).

682

683

684

Variable Matrix	Variable Type	Variable (unit)	Data Source
Neighbourhood	Structural diversity	Standard Deviation of Height (cm)	Schnabel <i>et</i> <i>al.</i> (2019)
	Identity	Number of Consp. Neighbours	Madsen <i>et al</i> .
		Number of Heterosp. Neighbours	Madsen <i>et al</i> .
	Competition	Mean Basal Area of Consp. Neighbours (cm ²)	Madsen <i>et al</i> .
Environmental	Topographic	Slope Intensity	Healy <i>et al.</i> (2008)
	Hydrologic	Length of Drainage Ditches (m) Average Water Table Depth (cm)	Healy <i>et al.</i> (2008) Healy <i>et al.</i> (2008)
	Edaphic	Soil Nitrogen (%)	Madsen <i>et al</i>

Table 1 Selected neighbourhood and environmental variable matrices.

Note: The variable Slope Intensity ranked plot slope as 1 = flat, 2 = medium, 3 = steep. Response variables included 4 observed and 3 predicted root traits: observed traits were number of primary roots, length of excavated root (LERoot), specific root length (SRL), and the ratio of the number of secondary roots to primary root length (Secondary Root Branching Intensity), and predicted root traits were the mean effective radius of the root system (EfRadSys), the total length of root system (TLR), and estimated coarse root biomass (CRB). Neighbourhood variables were calculated for the nearest neighbours (maximum: 8) of the focal trees; variable means were

subsequently calculated for each plot (N = 21).

695	The environmental variable matrix consisted of topographic, hydrologic and edaphic
696	variables that were collected in 2017 or earlier. Topographic variables included slope direction
697	and intensity, plot position, and elevation, all of which were recorded in 2005 (Healy et al.,
698	2008). Slope intensity of a given plot was ranked as 1 (flat), 2 (medium slope) or 3 (steep slope),
699	and plot position was defined as 1 (top of a hill), 2 (on slope) or 3 (bottom of the hill).
700	Hydrologic variables included the number and length of drainage ditches (m), and the maximum,
701	minimum, variance and average depth to water table (cm) (Healy et al., 2008). Depth to water
702	table was recorded every two weeks since 2005 using 2-inch PVC piezometers buried to 50cm

703 depth, four per plot; water table variables used in the CCA were averages of values from 2005 to 2017. In 2017, we gathered four soil samples in each plot, totalling 88 samples following the 704 methodology of Abraham (2004). Samples were collected at the vertices of a 15m² grid nested 705 within the plot. These soil samples were analyzed for dry bulk density, pH, and soil percent 706 organic carbon and nitrogen at the UC Davis Stable Isotope Laboratory 707 708 (https://stableisotopefacility.uc davis.edu/). Table S4 in Supplementary Material presents all 709 independent environmental variables considered for the CCA. The variables selected from the 710 environmental matrix included slope intensity, the length of drainage ditches (m), the average 711 depth to water table (cm), and soil percent nitrogen (Table 1). Correlation between these variables was tested with Pearson's product-moment correlation tested and the strongest 712 correlation (between the length of drainage ditches and the average depth to water table) was 713 714 found to be statistically insignificant (p-value of 0.1667).

Variance partitioning was carried out to compare the amount of variance uniquely
explained by the neighbourhood and environmental CCAs, as well as the shared variation that
they explained. We used the function "varpart" from the "vegan" package (v.2.5-2) (Oksanen *et al.*, 2018).

719 **Results**

720 3.1 Understanding the Sources of Variation in Root Traits

We used Pearson correlations to test for allometric trade-offs between primary root number, length, diameter, and secondary root branching intensity of the excavated roots. While the correlation between the number of primary roots and primary root length was not significant, the number and diameter of primary roots were found to vary together, such that trees with more roots tended to also grow thicker roots (correlation of 0.24, p-value: 0.006). In contrast, as trees'
726	primary roots grew longer, the number of secondary roots branching off the primary roots
727	decreased (correlation of -0.37, p-value < 0.001). The strongest correlation was found between
728	root length and diameter, indicating that as a tree's roots became thicker, they also tended to
729	grow longer, or vice versa (correlation of 0.56, p-value < 0.001).
730	While we failed to detect any significant mixture main effects at the individual tree level,
731	the species identity nested under mixture effect were statistically significant for the Length of
732	Excavated Roots (LERoot), the secondary root branching intensity, and the predicted Effective
733	Radius of Root systems (EfRadSys) (Table 2, Figure 2). The length of excavated roots (LERoot)
734	of AE and TR were significantly greater than that of LS in monoculture (71.2% and 74.7%
735	greater, respectively), in 3-species mixtures (65.4% and 68.6%, respectively), and in 5-species
736	mixtures (52.7% and 55.3%, respectively), as shown by post-hoc Tukey tests that used a
737	significance level of $\alpha = 0.05$. The trees with the highest frequency of secondary roots arising
738	from primary roots were CO in monoculture, which exhibited 251% the average number of
739	secondary roots per meter of primary root. Effective root system radius (EfRadSys) estimates of
740	different species fell into three different groups: AE and TR had the largest root system extents,
741	CO and HC had intermediate ones, and LS had the smallest; only the first and last of these
742	groups were found to be significantly different (Figure 2).

Larger trees grew more extensive root systems than smaller trees, though several root traits were suppressed in focal trees growing beside taller neighbours. The ANCOVA indeed showed that increasing focal tree size had a significant, positive effect on all root traits except secondary root branching intensity (Table 2, Figure 3). Conversely, after accounting for focal tree size in the model, we found that neighbour trees that were taller than the focal trees had a significant and negative effect on LERoot, the specific root-length (SRL), and EfRadSys (Table

2, Figure 4). Estimates of coarse root biomass (CRB) were not significantly affected by any

independent variable or covariate except for focal tree size, where larger focal trees tended to

751 have greater CRB estimates.

Table 2 F-values and their significance levels of ANCOVA tests of dependent root traits with
independent variables including mixture treatment (1, 3 or 5 tree species per plot), species
identity nested under mixture, and plot nested under species identity nested under mixture.

	Mixture (d.f. 2)	Species (Mixture) (d.f. 12)	Plot[Species (Mixture)] (d.f. 32)	TreeSize (d.f. 1)	RelHeight (d.f. 1)
Part A					
(Observed)					
No. of 1° Roots	0.15 ns	1.57 ns	1.76 *	36.7 ***	1.6
LERoot	8.59 ns	4.02 *	1.82 *	72.0 ***	10.8 **
SRL	2.23 ns	3.60 ns	2.36 **	17.1 ***	9.67 **
2° Root	5.65 ns	8.29 ***	1.41 ns	2.84 ns	1.18 ns
Branching Int.					
Part B					
(Predicted)					
EfRadSys	22.1 ns	6.25 ***	1.20 ns	241 ***	22.8 ***
TLR	2.50 ns	1.61 ns	2.20 **	132 ***	0.56 ns
CRB	1.73 ns	1.48 ns	0.70 ns	88.6 ***	0.66 ns

755 Note: Observed root traits include the number of primary roots, the length of excavated roots (LERoot), the specific root length (SRL), the secondary root branching intensity (number of 756 757 secondary roots per meter of primary root). Predicted root traits include the effective radius of the root system (EfRadSys), the total length of the root system (TLR), and the estimated coarse 758 root biomass (CRB), all at the level of individual focal trees. Covariates include focal tree size 759 (diameter at breast-height) of the focal tree and the difference between focal tree height and the 760 mean height of their closest neighbours (max: 8 neighbour trees). (N = 128 focal trees). 761 Significance levels: *, P < 0.05; **, P < 0.01; ***, P < 0.001; ns, not significant. 762

763





Fig. 2 Least squares means of the observed length of excavated roots (LERoot) and secondary 767 root branching intensity (number of 2° roots per meter of 1° root, SecRootBrInt), and the 768 predicted effective mean radius of the root system (EfRadSys). Error bars represent upper and 769 lower 95% confidence limits as calculated by the least square mean estimation (N = 128 sample 770 771 trees).



Fig. 3 Significant effects of focal tree size (represented by diameter at breast-height) on root
traits; units of traits reported after trait names. Observed root traits include the number of
primary roots, the length of excavated roots (LERoot), and the specific root length (SRL).
Predicted root traits include the effective mean radius of the root system, the total length of root
systems, and coarse root biomass (CRB) estimates at the individual tree level (N = 128 focal
trees). Black lines are simple linear regression fits with standard error represented as grey
margins of lines; "p" refers to p-values.





790 3.2 Effects of Mixtures and Competition on Root Traits

791 The biplot in figure 5 allowed us to examine how the dependent root traits (number, length, and diameter of primary roots, secondary root branching intensity, and the predicted 792 793 effective radius of root systems, total length of roots, and coarse root biomass) respond to a number of independent variables. It shows that trees had thicker, longer primary roots but a 794 lower number of primary roots in neighbourhoods with more heterospecific neighbours (Table 3, 795 796 Figure 5). Conversely, focal trees surrounded by more, and larger, conspecific neighbours tended to have more primary roots that were thinner, suggesting a trade-off between primary root size 797 798 versus primary root number. Heterogeneity in neighbour height positively affected secondary

799	root branching and decreased specific root length. The amount of variation in root traits
800	explained in the neighbourhood CCA was 63.0%. The first axis, which explained 58%, was
801	mainly determined by the mean basal area of conspecific neighbours, as well as the number of
802	heterospecific neighbours (Table 3). The second axis was primarily explained by the number of
803	heterospecific and conspecific neighbours and explained an additional 4% of root trait variation

804	Table 3 Axis loading factors of Canonical Correspondence Analyses that relate neighbourhood
805	and environmental matrices with observed root traits.

Variable Type	Variable	Axis 1 Loading Factor	Axis 2 Loading Factor
	Standard Deviation of Height (cm)	0.36	-0.18
N	Number of Conspecific Neighbours	0.17	0.53
Neighbourhood	Number of Heterospecific Neighbours	-0.42	-0.85
	Mean Basal Area of Conspecific Neighbours (cm ²)	-0.76	0.14
	Slope Intensity	-0.23	-0.58
Environment	Length of Drainage Ditches (m)	0.14	-0.11
Environment	Average Water Table Depth	-0.27	0.46
	Soil nitrogen (%)	0.32	-0.60
			-

Note: The root traits used in the dependent variable matrix include the length of excavated roots (LERoot), the number of primary roots per tree, the diameter of excavated roots, the specific root length of excavated roots (SRL), and the number of secondary roots on excavated primary roots. Variable means calculated at the plot level; for each axis and variable type, table presents the three variables with the highest axis loading factors in **bold** (N = 21 plots, excluded plot AE2).



Fig. 5 Canonical Correspondence Analysis of observed root traits with neighbourhood indices, 812 including: the length of excavated roots (LERoot), the diameter of primary roots (RootDiameter), 813 the number of primary roots (Number1°Roots), the specific root-length (SRL), and the number 814 of secondary roots per meter of excavated primary root (2°RootsPer1°Root). Neighbourhood 815 816 variables include the number of conspecific neighbours (NumConsp), the number of 817 heterospecific neighbours (NumHeterosp), the standard deviation of height (sd_h_N), and the 818 mean basal area of conspecific neighbours (meanConspBA), all of which were calculated for "neighbourhoods" of the 8 nearest neighbours of the focal trees; variables then averaged at the 819 plot level. Total variance explained was 63.0%, of which the first axis explained 57.9% and the 820 second axis explained an additional 4.1% (N = 21 plots). 821

The CCA biplot (Figure 6) shows that the length and number of primary roots responded differently to slope intensity and soil nitrogen. Trees growing on more intensely sloped soil had more, yet shorter, primary roots and more secondary roots per meter of primary root. Higher soil nitrogen was correlated with fewer, longer primary roots and fewer secondary roots. In plots with a higher average depth to water table, trees had shorter primary roots but more primary and
secondary roots. Finally, trees in plots with longer ditches for water drainage tended to have
fewer, longer roots (Figure 6). The amount of variation in root traits explained by the
environmental variables in the CCA was 30.4%. The first axis of ordination, which explained
21.0% of the variation, was principally determined by soil nitrogen, average depth to water table,
and slope intensity, while the second axis, which explained an additional 9.0% of variation, was
largely determined by slope intensity (Table 3).



833

Fig. 6 Canonical Correspondence Analysis relating observed root traits to environmental
characteristics. The observed root traits include the length of excavated roots (LERoot), the

diameter of primary roots (RootDiameter), the number of primary roots (Number1°Roots), the

specific root length (SRL), and the number of secondary roots per meter of excavated primary 837 838 root (2°RootsPer1°Root). Environmental variables include the intensity of slope (SlopeIntensity), 839 where 1 indicates flat, 2 indicates medium slope and 3 indicates steep slope, the length of waterconducting ditches (DitchL), the average water table depth (WaterTableDepth), and percent soil 840 841 nitrogen (N_percent). Variable means calculated at the plot level. Total variance explained was 30.4%, of which the first axis explained 21.0% and the second axis explained an additional 9.0% 842 (N = 21 plots).843 844 The coarse root traits of focal trees showed a much greater response to neighbourhood than to environmental, characteristics. Neighbourhood and environmental matrices together 845 846 explained 77.8% (adjusted R-squared of 55.6%) of the variation in the observed root traits. The

overlap in root trait variation explained by the two matrices was only 8.8%, while the percentage

- 848 of variation in root traits uniquely explained by the neighbourhood variables was 40.8%, and
- environmental variables alone explained only 6.0% of variation in root traits (Figure S1 in
- 850 Supplementary Material).

851 **Discussion**

4.1 Root responses to neighbour size and identity

Unsurprisingly, focal tree size was an important factor for all the root traits we tested, as 853 larger trees tended to have more extensive root systems composed of more numerous roots than 854 did smaller trees. Tree size has been shown to affect traits such as crown width and diameter 855 856 (Poorter *et al.*, 2006) and root traits such as the number of roots per root system, though perhaps not root diameter (Zanetti et al., 2015). Relative tree height (RelHeight, the mean height of 857 neighbour trees compared to focal tree height) played an opposing role, such that taller 858 859 neighbour trees apparently restricted focal tree root length and extent. This confirms our first 860 hypothesis, which proposed that taller neighbour trees suppress focal tree root length, suggesting that asymmetric competition for light between crowns had a negative effect on the root effective 861 862 length, specific root length, and predicted root system extent. This might also explain why, as

tree height diversity increased (heights differed more between trees in a neighbourhood), focal
tree root length decreased and the number of secondary roots per meter of primary root
increased. Such tree height diversity in neighbourhoods has been shown to occur when dominant
trees asymmetrically outcompete their smaller neighbours (Kuuluvainen *et al.*, 1998). Therefore,
our results add to the evidence that above-ground, asymmetric competition for light leads to
whole-plant growth suppression of smaller trees.

In Sardinilla, a root growth trade-off depending on neighbour identity occurred, where trees either grew many, shorter lateral roots in the presence of conspecifics or they grew fewer but longer and thicker lateral roots when growing with heterospecifics. This trade-off is in line with previously published results that found that annual herbaceous plants reduced investment in root length and root system size when growing with conspecifics (Dudley & File, 2007; Murphy & Dudley, 2009).

We confirmed our second hypothesis, which proposed that tropical tree roots extend 875 876 further in mixed stands than in monocultures, possibly due to competitive reduction belowground. The work of Belter and Cahill (2015) provides a theoretical foundation to understand our 877 observations: they measured the response of 20 tree species of 30-day old seedlings' root 878 879 systems to the presence of neighbours, highlighting two root "behavioural" strategies. The first is size-dependency, or the horizontal reduction of root systems to avoid competition with 880 881 neighbours. The second is location-dependency, or spatial plasticity in root placement in response to neighbour presence. Although Belter and Cahill worked in greenhouses, their 882 883 hypotheses help explain the results from our 20-meter-tall planted forest. When surrounded by conspecific neighbour trees, focal trees at Sardinilla pursued the size-dependency strategy, 884 constraining the horizontal extent of their root systems while increasing the total number of roots 885

in this smaller space. In this way, trees may both reduce conspecific below-ground competition 886 and maximize nutrient absorption in a smaller circle centered on the focal tree. Conversely, focal 887 888 trees growing in more species-rich neighbourhoods seem to have adopted the locationdependency strategy to develop their root systems, opting to modify root position in the soil and 889 grow longer roots to seek preferential patches of soil nutrients. Our results show that tree 890 891 neighbourhoods, in addition to their increasingly recognized role in explaining above-ground tree 892 growth (Fichtner et al., 2018; Schnabel et al., 2019), are a key determinant for coarse root 893 system growth and extent.

894

4.2 Soil nitrogen and water overabundance

895 Root length, number and branching pattern responded distinctly to nitrogen availability and waterlogging. Focal trees in Sardinilla tended to have longer and fewer primary roots with 896 fewer secondary roots in more nitrogen-rich soil. This finding may perhaps be generalized to 897 898 other tropical forests, as soil nitrogen content at the Sardinilla site is similar to other tropical soils: Moore *et al.* (2018) sampled the top 10 cm of soil in Sardinilla and reported a range of 899 mean soil nitrogen mass from 0.28 kg m⁻³ to 0.25 kg m⁻³ (or 0.46%) in 2001 and 2011, 900 901 respectively. Barro Colorado Island, which is located in Panama and serves as a good comparison due to its relatively close location and similar climate (Delagrange *et al.*, 2008), was 902 found to have a mean soil nitrogen mass of 0.23 kg m⁻³ (Moore et al., 2018). Similarly, Marin-903 Spiotta et al. (2009) reported values of 0.24 kg m⁻³ for tropical forests undergoing regrowth for 904 80 years in Puerto Rico. Desnos (2008) described how model plant Arabidopsis' roots sense 905 nitrate (NO_3) via a complex biochemical pathway and alter root system architecture in response: 906 secondary root growth from primary roots was suppressed while primary root growth was 907 908 stimulated in patches of higher nitrate (Zhang et al., 1999). We observed a similar correlation

between higher soil nitrogen and primary root growth with secondary root suppression,

910 suggesting a similar response in both young, herbaceous roots and coarse roots of tropical trees,911 assuming that soils higher in total N would have had higher nitrate.

912 Plant root traits such as rooting depth and length of lateral roots are determined by 913 evolution at the species level and phenotypic responses at the individual level to local water and 914 nutrient stresses (Chapin et al., 1993; Paz et al., 2015). Markesteijn and Poorter (2009) grouped 1-year old tropical seedlings by species into evolutionarily dry- and moist-adapted functional 915 916 groups, the former with deeper roots to access deeper soil water while the latter tends to grow 917 longer, branching lateral roots to absorb shallow soil water. Van der Weele et al. (2000) 918 observed a plastic reduction in lateral roots of Arabidopsis thaliana plants that were placed under 919 water stress, providing an example of how individual plants can react to local environmental conditions.. Although Valverde-Barrantes et al. (2013) found that soil factors and water 920 availability had relatively little impact on 7 root traits in a temperate forest, we observed 921 922 different root growth patterns depending on local water table depth, suggesting that watertable level is related to water availability. Although we could confirm our third hypothesis (that 923 924 neighbourhood characteristics explain more variation in root trait variation than abiotic 925 characteristics), we found that roots also responded plastically to their abiotic environments in a 926 complex fashion. This is in line with the work of Chen *et al.* (2018), who proposed that superior 927 water availability in tropical stands compared to temperate ones explained the greater variation 928 in coarse root traits they observed in the former. In Sardinilla, trees grew more, though shorter, 929 primary roots with many more secondary roots in plots with deeper water tables and steeper slopes, both of which may represent soil conditions in which the topsoil horizons are sufficiently 930 well aerated or drained. Indeed, soil depth has been shown to strongly affect root system 931

architecture and depth (Marden et al., 2016). Trees in Sardinilla in plots with deeper water tables 932 933 may have had more numerous primary and secondary roots due to more favourable soil 934 conditions for root growth. The site is characterized by mild slope, so we think it unlikely that focal trees grew more primary roots for increased stability against wind (Tobin et al., 2007), 935 936 gravity, or erosion (Reubens et al., 2007). However, we may have observed the phenomenon 937 described by Ghestem et al. (2011) in which trees produce coarse roots on slopes to facilitate water drainage as water flows in channels formed around roots. It is worth noting that the 938 939 Sardinilla site receives a large amount of precipitation in the wet season, resulting in seasonal 940 waterlogging in lower plots (Kunert et al., 2012). Therefore, it is possible that different seasonal patterns in water table depth between plots could have had affected the focal tree root systems 941 (mean depth to water table and species distributions depicted in Figure S2 in Supplementary 942 Material). For example, our results suggest that trees in seasonally waterlogged plots may invest 943 944 in fewer but longer primary roots, possibly to try to find more suitable, better aerated patches of 945 soil.

946 Conclusions

This paper contributes to the scarce literature of how coarse root traits and root systems 947 948 of adult-sized trees interact with neighbours and environmental conditions along a tree species richness gradient. We found that the size of conspecific neighbours, neighbourhood species 949 950 composition, and variation in tree height at the neighbourhood level explained most of the variation in coarse root traits of mature trees. Our findings demonstrate plastic changes in root 951 952 traits in response to neighbour identity and certain environmental conditions. For example, trees 953 grew less broad root systems with more numerous coarse roots when growing in soil with deeper average water tables and when growing with more conspecific trees in the local neighbourhood, 954

while the reverse was true in neighbourhoods with a mixture of species and in soils where the
water table was closer to the surface. Such commonalities in the plasticity of mature tree root
systems may point toward strategies employed by tropical tree roots in certain suites of growing
conditions, lending support to theories of how plants reduce the amount of root competition they
experience by avoiding neighbour roots through altering their distribution in the soil (e.g. Belter
and Cahill, 2015).

962 Acknowledgements

963 We would like to thank colleagues in Panama, Germany and elsewhere for their essential contributions in making this research effort possible. Field work, including the months of hard 964 965 work necessary for the excavation of lateral roots and root crowns, was made possible with the 966 help of J. Monteza the Sardinilla site manager, L. Mancilla the coordinator of the harvest, J. A. Zepeda A. who supervised root excavation as well as the entire field crew. Many thanks to them 967 968 all. Constructive comments on the manuscript were given by TreeDivNet scholars, in particular 969 J. Guillemot, M. Kunz, K. Norbert, L. Schwendenmann, Y. Oelmann, and A. Fichtner. The 970 research was funded by an NSERC Discovery grant to CP as well as by her Canada Research Chair. CM acknowledges a fellowship from the NSERC Create Biodiversity, Ecosystem 971 972 Services and Sustainability program and field support from the Centre D'étude de la Forêt. FS 973 was supported by the International Research Training Group TreeDì funded by the Deutsche 974 Forschungsgemeinschaft (DFG, German Research Foundation) – 319936945/GRK2324. The long-term support of the Sardinilla plantation by the Smithsonian Tropical Research Institute was 975 essential. 976

978 Supplementary Material

Table S1. Seven potential methods from the literature that were essayed to predict the length of

980 unexcavated roots in Sardinilla. The variables used and goodness-of-fit values of the model

papers presented in grey while those of Sardinilla are presented in white for comparison. N = 128focal trees.

Authors	Method	Predictor	Goodn	Goodness	Sardinilla	Applied to
		Variables Used	ess-of-	-of-fit	Species	Sardinilla data
		by Author(s)	fit			
			Metric			
Kalliokos	OLS	Natural log of	\mathbb{R}^2	0.66	AE	0.9313
ki et al.,	regressio	root diameter			TR	0.9456
2008	n,				LS	0.9445
	Intercept				HC	0.8730
	forced to 0				СМ	0.9069
Smith et	OLS	Diameter at	R ²	0.721	AE	0.307
al. 2014	regressio	breast height			TR	0.5593
	n				LS	0.4454
					HC	0.07945
					СМ	0.4554
Horne et	RMA	Diameter at	R ²	0.72	AE	0.1929
al. 2015		breast height			TR	0.5425
					LS	0.3632
					HC	0.1761
					СМ	0.4297
Zuur et	GAMM	Diameter at	AIC _C	107.06	AE	51.354
al., 2009;		breast height,			TR	33.715
Vicente et		Root Diameter,			LS	40.114
al. 2006;		Tree Height			HC	62.249
Bomford					CM	54.195
et al.,	GLM	Diameter at	AIC	456.4	AE	51.354
2010;		breast height,			TR	33.715
Galvez-		Root Diameter			LS	40.114
Ceron et		(with random			HC	62.249
al., 2012;		effects), Tree			СМ	54.195
Yee et al.		Height				
1991	GAM	Diameter at	\mathbf{R}^2		AE	0.307
		breast height,			TR	0.559
		Root Diameter			LS	0.445
		(with random			HC	0.0794
		effects), Tree			CM	0.455
II.1.	Dent' 1	Height	D			0.66101, 1.000
Heisen et	Partial	19 functional	K-sq;		AE	0.00181; 1.992 m
al. (2016)	least	traits to predict	RMSE		IK	0.23009; 3.845 m

squares	root length	0.699;	LS	0.301276; 2.076 m
regressio	density (RLD)	21.708	HC	0.085072; 3.973 m
n		km/m ³	CM	0.25118; 3.806

Table S2. Five species-specific predictive models developed via partial least squares regression.

Species	Comp	Var explained	RMSEP (m)	Mean
Species	number	(%)		Excavated
				Root Length
				(m)
AE	5	47.09	3.845	8.754
CO	3	43.88	3.424	6.778
HC	2	26.43	3.962	6.014
LS	4	46.11	2.076	5.839
TR	5	75.25	1.992	7.457

985 Note: Species include Anacardium excelsum (AE), Cedrela odorata (CO), Hura crepitans (HC),

986 Luehea seemannii (LS), and Tabebuia rosea (TR). Variables include: "Comp. number," which

987 indicates the number of uncorrelated components; "Var explained," which is the amount of

variation explained by the final PLSR model; the Root Mean Standard Error of Prediction

989 (RMSEP); and the mean excavated root length. Variable coefficients differ in each model

990 component, and thus aren't included (N = 128 focal trees).



- 992 Figure S1. Variance partitioning of canonical correspondence analyses relating dependent root
- traits and two matrices of independent variables: plot-level environmental characteristics and
- neighbourhood variables including number of heterospecific and conspecific neighbours,
- standard deviation of neighbourhood tree height, and the mean size of conspecific neighbours;
- amount of variation explained presented with adjusted R-squared values.



Figure S2. Predicted effective root system radius, depth to depth to water table and directionality
of slope (black arrows). Study species include *Anacardium excelsum* (AE), *Cedrela odorata*(CO), *Hura crepitans* (HC), *Luehea seemannii* (LS), and *Tabebuia rosea* (TR). N = 128 focal
trees.

1004 Partial Least Squares Regression

PLSR projects predicted and predictor variables into new space, decomposing these observable variables into latent structures, which are then used in a linear regression (Haenlein & Kaplan, 2004). Final models were selected using cross-validation and minimizing the root mean squared error of prediction (RMSEP). These models were constructed with the "pls" package in R (Mevik *et al.*, 2019), and were used to predict root lengths with the package 'forecast' (Hyndman *et al.*, 2019).

1011 A conceptual diagram illustrates our decision process for choosing PLSR over the other 1012 potential models and methods (Figure S3). We used data of previously excavated root systems in 1013 Sardinilla (Sinacore et al., 2017) to validate PLSR-model predictions. These data were gathered 1014 in 2009, when 40 trees in Sardinilla were entirely excavated, including their root systems, to 1015 describe root system architecture and develop allometric biomass equations for 6 tropical 1016 species. Their study included Anacardium excelsum, Cedrela odorata, and Tabebuia rosea, on 1017 which the present study focuses. Models were derived from a subset of these fully excavated root systems (roughly 16% of roots used to predict 84% of dataset) that was proportional to the 2017 1018 1019 dataset in terms of observed versus predicted root lengths. The root mean squared error of 1020 prediction (RMSEP) was found to not differ significantly between the dataset of Sinacore and 1021 our dataset (paired t-test p-value: 0.2473, 1000 iterations).

In partial least squares regression, model predictor variables are reduced to an optimal number of uncorrelated components ("Comp. number") with which to predict root length. The ideal number of components maximizes the training set variance explained ("Var explained") and minimizes the Root Mean Standard Error of Prediction (RMSEP). Results for Sardinilla trees presented in Table S3.



Figure S3. Partial Least Squares Regression (PLSR) was chosen to predict root length. This
method was compared to commonly used techniques, including Ordinary Least Squares (OLS),
Reduced Major Axis Regression (RMA), Generalized Linear Models (GLMs) and Generalized
Additive Models (GAMs). Green arrows denote satisfactory aspects of modelling techniques,

and red arrows represent significantly problematic aspects of modelling techniques. Relevant

drawbacks of these latter techniques cited from the literature (1. Haenlein and Kaplan, 2010; 2.
Reinartz *et al.*, 2009; 3. Carrascal *et al.*, 2009, Ohsowski *et al.*, 2016), as well as strengths of

PLSR (1. Helsen *et al.*, 2016, Haenlein & Kaplan, 2010; 2. Carrascal *et al.*, 2009, Reinartz *et al.*,
2009).

1037

1038 Canonical Correspondence Analysis

1039 Variables were scaled with the Hellinger transformation using the 'vegan' package in R

1040 (v.2.5-2; Oksanen, 2018) as recommended by Legendre and Gallagher (2001). A step-wise

1041 model selection algorithm native to the 'vegan' package, called 'ordistep', was used to select

1042	variables from the complete neighbourhood (Table S3) and environmental (Table S4) variable
1043	matrices for use in the CCAs. Variance partitioning (with the vegan package) was carried out to
1044	compare the amount of variance explained by the environmental and neighbourhood structure
1045	matrices. For dependent variables with greater than 0.80 correlation (Pearson's Rho), one
1046	variable was chosen to represent the group. For example, the number of primary lateral roots was
1047	chosen to also represent the total length of root systems (correlation of 0.843).
1048	Table S3. Complete tree neighbourhood variable matrix from which the four variables that

- explained the most variation in the dependent root traits were chosen for the final CCA by forward stepwise model selection.

Variable Type	Variable (unit)	Data Source
Structural diversity	Standard Deviation of Height (cm) Standard Deviation of Basal Area (cm ²) Gini Coefficient of Height Gini Coefficient of Basal Area	Schnabel et al. (2019)
Identity	Number of Consp. Neighbours Number of Heterosp. Neighbours Plot species richness	Madsen et al.
Competition	Total Basal Area of Consp. Neighbours (cm ²) Total Basal Area of Heterosp. Neighbours (cm ²) Total Basal Area of Consp. Neighbours (cm ²) Total Basal Area of Heterosp. Neighbours (cm ²) Mortality of Nearest Neighbours	Madsen <i>et al</i> .
	Hegyi Distance-Dependent Competition Index	Schnabel et al. (2019)

1054 Table S4. Sources of data, time of sampling and variable type of the complete environmental

1055	matrix, from which the four variables with the highest explanatory power were selected by
1056	forward stepwise model selection.

Sampling	Variable	Variable (Unit)	Data
Year	type		Source
2005	Topographic	Slope direction Slope type Plot position Elevation	Healy <i>et</i> <i>al.</i> (2008)
		Number of water ditches Length of water ditches	
2005 – 2017 (every 2 weeks)	Hydrologic	Maximum depth to water table Minimum depth to water table Depth to water table variance	Healy <i>et</i> <i>al.</i> (2008)
		Average depth to water table	
2001 (pre- experiment baseline)	Edaphic	Dry bulk density pH Soil organic carbon %	Abraham (2004)
2017	Edaphic	Soil nitrogen % Dry bulk density pH Soil organic carbon % Soil nitrogen %	Madsen <i>et</i> al.

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Linking Statement

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In Chapter 1 of this thesis, I assessed variation in coarse root traits in response to 1358 neighbourhood and abiotic characteristics. The greater impact of nearest neighbours on the tested 1359 traits, compared to that of abiotic characteristics, was illustrated by variance partitioning. This 1360 1361 analysis was based on certain assumptions of neighbourhood size; in addition, this chapter also investigated root trait variation as an isolated compartment, though it is one part of the whole 1362 1363 organism. Therefore, to test these assumptions and broaden the scope of the thesis to the whole-1364 tree level, in Chapter 2 I compare the response of crown and root system area and compactness 1365 to competition with neighbours and various abiotic characteristics. I provide a comparison of 1366 crown and root system extent, test the ability of the Hegyi distance-dependent competition index 1367 to explain variation in focal tree biomass, and identify which aspects of the five tropical tree 1368 species' neighbourhoods and abiotic environments most strongly influence crown and root 1369 system area and compactness. The first and second chapters are therefore linked, both with each 1370 other and also with research of biodiversity-ecosystem function in forests, which typically focusses on above-ground tree morphology and competition. 1371

An Assessment of the Extent and Influence of Neighbourhoods on Tropical Tree Crowns and Root Systems.

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1395 Abstract

Comparisons of above- and below-ground tree architecture and plasticity remain scarce 1396 in the literature of competition dynamics in forests. We combined terrestrial laser scans and an 1397 extensive root excavation campaign in the tropical planted forest Sardinilla with annual 1398 1399 measurements to test how the crowns and root systems of 128 tropical trees varied with 1400 neighbourhood and environmental characteristics. Crown and root system extent were compared, 1401 the Hegyi competition index calculated at three different neighbourhood extents (nearest 8, 1402 above- and below-ground neighbours) was assessed for its ability to explain focal tree biomass, 1403 and neighbourhood and environmental variables that explained the majority of the variation in 1404 crown and root system area and compactness (a measure of morphological homogeneity) were 1405 identified. Root systems were 2.6 ± 1.1 (standard deviation) times wider than crowns on average, 1406 competition at the near neighbourhood scale predicted focal tree biomass better than at the above- and below-ground neighbourhoods (\mathbb{R}^2 of 0.46), and neighbourhood characteristics 1407 outperformed environmental ones in explaining variation in crown and root system traits (65.8% 1408 and 26.0%, respectively). We highlight the importance of competition with the nearest eight 1409 1410 neighbours for the biomass and architectural traits of the crown and root system of young adult 1411 tropical trees.

1413 Introduction

1414 In their Tansley review, Poorter et al. (2012) differentiate between the essential functions performed by leaves, stem, and roots: energy is acquired and carbon fixed through 1415 1416 photosynthesis in the leaves; stems conduct water and nutrients between above- and below-1417 ground organs and raise leaves above obstacles to light interception (e.g. shade cast by 1418 neighbouring plants); and roots absorb soil nutrients such as nitrogen and water while providing 1419 physical stability by anchoring the plant in the soil. Plants compete with their neighbours for 1420 above- and below-ground resources (Attiwill and Adams, 1993; Casper and Jackson, 1997); 1421 indeed, plants that fail to capture sufficient quantities of these resources suffer from reduced growth rates (Burton, 1993; Canham et al., 2004; Martínez-Vilalta et al., 2007) or even mortality 1422 1423 (Coomes and Grubb, 2000). Competition occurs between plants both above- and below-ground, 1424 as reported by Canham et al. (2004), who found that crowding by neighbour trees explained 1425 more variation in growth rates of temperate tree species western hemlock (Tsuga heterophylla 1426 (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) than shading alone. Competition between plants is complex, as larger plants may outperform smaller 1427 1428 neighbours if the resource sought is predictable in its distribution, such as how the directionality of light favours its capture by tall plants that overshadow shorter neighbours (Schwinning and 1429 1430 Weiner, 1998; Pretzsch, 2014). In contrast to light, soil nutrients may exhibit a patchy 1431 distribution and thus their capture may not be as easily pre-empted by plant roots (Schwinning 1432 and Weiner, 1998). Below-ground competition occurs between neighbours of different sizes, including trees and herbaceous plants alike (Bouttier et al., 2014). Many studies of below-ground 1433 1434 competition have found it to be size-symmetric (Casper and Jackson, 1997; Cahill and Casper, 2000; Schenk, 2006; though see Lei *et al.*, 2012), which means that the competitive effect that a 1435
given plant exerts on its neighbours is proportional to its size and that larger neighbours are also 1436 affected by competition with their smaller neighbours; size-asymmetric competition is distinct in 1437 1438 that larger neighbours have a disproportionately strong competitive effect on smaller neighbours (Rasmussen et al., 2019). Although Rasmussen et al. (2019) did observe size-asymmetric root 1439 competition for nitrogen in a greenhouse experiment, this was likely due to the low fertility and 1440 1441 high depth of soil used in their experiment. These conditions may have rendered soil nitrogen pre-emptible for roots, rewarding plants that grew roots more quickly into deeper, richer soil. 1442 1443 The magnitude and mode of competitive interactions between neighbouring trees is also a 1444 function of the availability of soil resources (Coates et al., 2013; Pretzsch et al., 2015). In their review of competition in forests, Coomes and Grubb (2000) described how above-ground 1445 competition for light dominates in forests growing on soils that are rich in nutrients and water, 1446 while competition primarily occurs below-ground in poorer soils. Experimental evidence of this 1447 1448 phenomenon has been observed in greenhouse experiments (Lin et al., 2014) and in natural 1449 temperate forests (Pretzsch et al., 2015).

At the species level, varying soil nutrient levels may also alter hierarchies of tree 1450 competitive ability, as Cavard et al. (2011) observed for three temperate tree species across a 1451 1452 rich clay soil in Quebec and poorer tills in Ontario. Coates et al. (2013) also found that each of 4 species reacted differently to soil nutrient conditions, neighbour proximity and shading in a sub-1453 1454 boreal spruce forest in British Columbia. Furthermore, in their comparison of the productivity of 1455 five 2-species mixtures with their respective monocultures in temperate Europe, Toïgo et al. 1456 (2014) found that 6 of the 10 mixtures exhibited greater overyielding than their respective 1457 monocultures when growing on sites of lower productivity. Therefore, abiotic conditions and 1458 species assemblages interact to shape competitive interactions between trees. Variations in the

competitive abilities of plant species above- and below-ground are due to differences in their 1459 architectural and phenological traits (Kunstler et al., 2016) that may depend on their life history 1460 1461 (Burton, 1993). For example, *Quercus* trees compete weakly below-ground, likely because they allocate only a tenth of the biomass that three other temperate species allocated to their fine roots 1462 (Rewald and Leuschner, 2009). However, traits are plastic to a degree, and morphological 1463 1464 plasticity in crown (Jucker *et al.*, 2015) and root traits (Valverde-Barrantes *et al.*, 2013) may allow plants to better cope with biotic and abiotic stressors. For example, biomass can be 1465 1466 plastically redistributed between tree compartments. In the Sardinilla tropical planted forest, 1467 where the present study was carried-out, trees experiencing intense competition for light allocated more biomass to tertiary branches (Guillemot *et al.*, in review). Root traits have also 1468 been observed to vary strongly with environmental and neighbourhood characteristics (Valverde-1469 1470 Barrantes et al., 2013): root system architecture can vary strongly with soil texture (Zanetti et al., 2015) and hydrologic regime (Schenk and Jackson, 2002), and spatial segregation of different 1471 1472 species' fine and coarse roots can occur in mixtures (Bolte et al., 2013; Schmid et al., 2015; Rajab et al., 2018). 1473

Beginning in the 1960s (Newnham, 1964), individual tree models such as JABOWA (Bugmann, 2001) and GUESS (Smith *et al.*, 2001) began to be used to predict such phenomena as tree growth and mortality, largely based on their interactions with neighbours. In the early 2000s, a number of studies were performed to examine the size of neighbourhoods, or "zone of influence" (Bauer *et al.*, 2004; Uriarte *et al.*, 2004; Schneider *et al.*, 2006). Relatively few studies compare how this zone of influence differs above- and below-ground (Smith, 1964; Ashton, 1975; Hruska *et al.*, 1999; Malinovski *et al.*, 2015; Sinacore *et al.*, 2017). In response to this

1481 dearth of such analyses, our first objective was to carry out a comparison of crown and root1482 lateral extent for 16-year old tropical trees.

1483 Our second objective was to better understand the scale at which competition occurs at the neighbourhood level, for which we assessed which of three neighbourhood extents (near 1484 neighbourhood, above-ground neighbours and below-ground neighbours) best explain measured 1485 1486 focal tree biomass using a competition index. Studies of the effects of neighbour tree species 1487 identity and competition intensity on focal tree growth rates and recruitment indeed tend to use 1488 arbitrary, spatially homogenous neighbourhoods, the extent of which are typically validated with 1489 the lowest Akaike's Information Criterion (e.g. Punchi-Manage et al., 2015; Lu et al., 2015; Chi et al., 2017; Kramer et al., 2019). Neighbourhood characteristics (e.g. competitive intensity, 1490 shading, and species compositions) have been shown to significantly affect tree above-ground 1491 architecture (Sapijanskas et al., 2014; Jucker et al., 2015; MacFarlane and Kane, 2017; 1492 1493 Guillemot, in review, Kunz et al., in review) and below-ground traits (Valverde-Barrantes et al., 1494 2013). Our third objective was to identify which neighbourhood and abiotic characteristics explained more variation in crown and root system architecture. We hypothesized that 1495 1496 neighbourhood characteristics uniquely explain more variation in both crown and root system 1497 area and compactness than abiotic characteristics, as observed by Valverde-Barrantes et al. (2013). 1498

1499 Methods

1500 Study Site

The Sardinilla experiment, Colon district, Panama (9°19' N, 79°38' W) is a planted forest diversity experiment established in 2001 to compare tree monocultures with tree mixtures to assess their differences in ecosystem functioning. The species planted include *Anacardium*

excelsum (AE), Cedrela odorata (CO), Cordia alliodora (CA), Hura crepitans (HC), Luehea 1504 seemanii (LS), and Tabebuia rosea (TR), all of which are native species to Panama. Twenty-four 1505 plots including six 6-species plots, six 3-species plots, and twelve monoculture plots (two per 1506 planted tree species) were established, each of approximately 2025 m². One of the species, 1507 *Cordia alliodora*, exhibited high mortality soon after planting its two monoculture plots so it was 1508 1509 not included in final analyses (Schnabel et al., 2019). The majority of the annual precipitation (average of 240 cm) at the site falls during the rainy season between May and November 1510 1511 (Scherer-Lorenzen et al., 2007). Soil at the Sardinilla site is mostly a clay-rich Tertiary limestone 1512 with significant seasonal variation in soil moisture.

1513 Abiotic Environmental Characteristics

Depth to water table was recorded twice per month from 2005 to 2017 using PCV piezometers at 50 cm depth. Slope intensity was measured in 2005 (Healy *et al.*, 2008). Ditches were dug when the Sardinilla planted forest was established to facilitate drainage in certain plots. In 2017, we gathered 88 samples (4 per plot) following the methodology of Moore (2018). These soil samples underwent chemical analysis to quantify nitrogen percent, organic carbon percent, soil acidity, and soil dry bulk density at the UC Davis Stable Isotope Laboratory (https://stableisotopefacility.uc davis.edu/).

1521 *Laser Scanning and Crown Architecture*

1522Terrestrial Laser Scanning (TLS) enables highly detailed analyses of above-ground tree

architecture that are otherwise extremely difficult to carry out, such as quantifying the volume of

1524 tertiary branches (Guillemot *et al.*, in review). TLS was performed on the site in May and June of

- 1525 2017, 16 years after planting, using a RIEGL VZ-400i terrestrial laser scanner (Fa. Riegl,
- 1526 Austria) with full-waveform analysis capabilities. Data are characterized by high resolution:

separate points are collected at around 7 mm at 10 m distance from the scanner. We chose a laser
pulse rate of 600 kHz and a wavelength of 1550 nm to better sample the dense canopy which
characterized some plots. Each plot was scanned from 16 different scan positions, and each
scanning position was 10 meters apart. Because the scanner had a 360° field-of-view horizontally
and 130° field-of-view vertically, it was necessary to scan twice at each point to capture tree
architecture vertically. During the 13 days of scanning, local weather conditions were dry with
little wind and temperatures of approximately 25°C.

1534 Point-cloud registration (correct positioning of scans relative to each other) was performed using RiSCAN Pro (version 2.6.2). Error in relative registration was 5 mm at most for 1535 1536 each plot, and this error was characterized by a normal distribution and around a zero mean. The point-clouds of 128 trees from 22 plots were manually extracted from the point-clouds of 1537 neighbouring trees and vegetation using RiSCAN Pro software. These trees were destructively 1538 1539 harvested after scanning, yielding crown and root data; these 128 trees are hereafter referred to as 1540 the "focal trees". Two-dimensional (2D) crown projection areas for the focal trees were computed using the 2D-alpha-shape (α =0.5) of the projection of the crown points into the XY-1541 1542 plane. The 128 2D tree crown shapes were imported into QGIS (v.3.8.3) and tree crown 1543 projection area was measured. This variable represents the size of focal tree crowns.

1544 Tree Harvesting, Root Data Collection and Length Prediction

Following laser scanning, 128 trees stratified in three classes of growth rate: slow, medium and fast, were destructively harvested in 2017. Their above- and below-ground compartments were separated into categories including stem, primary, secondary and tertiary branches and leaves, root crown, etc., and their biomass was measured (Guillemot *et al.*, in review). The core of the root system within 50 cm from the stem was excavated, dried and weighed (see Madsen et al. (in review) for further details). The measured above- and belowground biomass values were summed for each focal tree. One of the primary lateral roots was
chosen at random and excavated and served to predict unexcavated lateral roots using their
diameters (Madsen *et al.*, in review) (Eq. 1).

$$L_R = D_R + DBH + D_{base} + H \tag{1}$$

Where L_R denotes root length (observed or predicted), D_R represents lateral root diameter, DBH is the focal tree diameter at breast-height, D_{base} is the focal tree's diameter at 10centimeter height, and H is the focal tree height; all variables are recorded and calculated in meters. Observed and predicted effective root lengths served to estimate focal tree root system extent and area. Focal tree crown and root system mean extent were used for a direct comparison of radial extent, and to identify potential crown and root system neighbours.

1561 Crown and Root System Compactness

Trees have been shown to exhibit morphological plasticity in their crown architecture to 1562 1563 minimize competition with neighbours (Schröter *et al.*, 2012), especially in species mixtures 1564 (Sapijanskas et al., 2014; Jucker et al., 2015). To represent such plasticity, we calculated indices 1565 of crown and root system compactness at the tree and plot levels. Crown compactness was computed using the 2D-alpha-shape approach as described in Kunz et al. (in print). It represents 1566 the degree of variation in the lateral distribution of branches in the crown, where higher values of 1567 crown compactness imply lower plasticity expressed. In short, the crown compactness measure 1568 1569 compares the crown projection area to its perimeter, such that a perfectly circular crown would be described with a value of ~ 1 , while a crown with greater perimeter for the same area (i.e. 1570 1571 more complex crown shape) would be described with a value less than 1 (Eq. 2) (Figure 1). Root

system compactness was calculated as the coefficient of variation in the diameters of its lateral
roots where they arise from the tree's stem; focal trees with lateral roots of more similar
diameters, and thus smaller coefficients of variation, were classified as having more compact, i.e.
homogenously shaped, root systems.

1576
$$Crown Compactness = \frac{Area}{Perimeter^2} 4\pi$$
 (2)

Plot level coefficients of variation of focal tree crown and root system compactness were 1577 calculated, and these variables were used to present plot-level variation in focal tree root system 1578 and crown shape. Of the 22 plots in Sardinilla, AE2 and HC2 were excluded from these 1579 1580 calculations either because of a lack of some vital root data or because their focal trees had only one root each, rendering it impossible to calculate the plot-level coefficient of variation of root 1581 1582 system compactness. Therefore, 20 plots were used and presented in this paper. We used these variables to represent and compare morphological plasticity in focal tree crowns and root 1583 1584 systems.

1585 *Competition Indices*

The competition experienced by focal trees was estimated using the Hegyi distancedependent competition index (Hegyi, 1974; Sharma *et al.*, 2016). The index uses focal and neighbour trees' diameters at breast height and distances from a given tree to estimate the competition it experiences from a given neighbour tree. The index ranges from 0 to 1, where 0 represents a lack of competition with neighbours while a 1 signifies intense competition with neighbours experienced by a focal tree. A neighbour's competitive effect on the focal tree increases with increasing neighbour size (diameter at breast height) and decreasing distance from the focal tree (Eq. 3). For each focal tree, we summed the Hegyi competition index for allneighbour trees (Figure 2).

1595
$$Hegyi = \sum_{i=1}^{n} \frac{DBH_j}{DBH_f * Dist} \quad (3)$$

Where DBH_j is the diameter at breast-height of a given neighbour tree in meters, DBH_f is the diameter at breast-height of the focal tree in meters, Dist is the distance between the given neighbour and the focal tree in meters, and *n* is the number of live neighbour trees. Three spatial scales were used to identify potential competitors: near neighbourhood, above-ground neighbourhood (AGN) and below-ground neighbourhood (BGN).

The first spatial scale, near neighbourhood, included only immediately adjacent live trees within a fixed radius of 4.5 meters (maximum: 8), which due to their proximity may exert a relatively large effect on the focal tree. For each focal tree, we used its spatially explicit twodimensional crown shape to identify all neighbour stems that intersected with its crown; the AGN was composed of these intersected trees. The BGN included all those neighbours whose stems grew within the predicted effective root system radius. In contrast to the constant radius of the near neighbourhood, the AGN and BGN s varied with focal tree size.

1608 Statistical Analyses

To address out first objective of comparing crown and root system size, we tested for a significant difference between focal tree crown and root system mean extent for all focal trees using a Student's paired T-test in R (v. 3.5.3). Mean crown extent was calculated for each focal tree using the area of its crown 2D-alpha-shape; this simplification from the real crown shape to an average extent value using the crown shape area and the relationship between area and the radius of a circle. We carried out this transformation to facilitate mean extent comparisons between crown and root systems. To test for an effect of species identity, we used an analysis of variance (ANOVA) with crown or root system mean extent as the dependent variables and compartment type (i.e. crown or root system) and species identity as two independent categorical variables; we used the same ANOVA model to test for an effect of species identity on crown and root system compactness at the tree level. We also tested for significant differences between species means of extent and compactness of the two compartments using the "agricolae" package (v.1.3-1, Mendiburu, 2019) in R.

For our second objective of comparing near neighbourhood, AGN and BGN in terms of their ability to explain focal tree biomass, we used linear regression in R. We compared the strength of the relationships between focal tree biomass and the Hegyi competition indices calculated at the three neighbourhood scales.

1626 Canonical Correspondence Analysis

For our third objective, we used Canonical Correspondence Analyses (CCA) and 1627 1628 variance partitioning from the "vegan" package (Oksanen et al., 2018; v.2.5-2) to compare the total amount of variation that matrices of neighbourhood and abiotic environmental 1629 1630 characteristics could explain. Two CCA and variance partitioning were run to compare the effect(s) of independent variables including (1) competition, neighbour species identity, and plot-1631 1632 level species mixture, and (2) environmental characteristics on crown and root system traits. In 1633 both CCAs, the dependent matrix included the plot-level mean of focal trees biomass, crown area, root system area, plus the plot-level coefficient of variation in root and crown compactness. 1634 1635 The first CCA was initially based on a matrix of neighbourhood and plot characteristics

1636 including 10 plot-level variables: species mixture treatment, mean focal tree biomass, the

presence or absence of the five study species, and the Hegyi competition indices at the near neighbourhood, AGN and BGN. Variables were selected for inclusion or exclusion from the CCA by the stepwise model building function "ordistep", in the "vegan" package (v.2.5-2), which uses permutation tests to include of exclude each independent variable; variables are kept in the model only if the permutation p-value is less than 0.05. The final CCA included the Hegyi competition index at the near neighbourhood and BGN, as well as the presence of absence of CO, AE and LS in the plot.

1644 The second CCA related variation in crown and root traits with environmental characteristics: the average of depth to water table measurements taken twice a month from 2005 1645 until 2017, slope intensity (1 =flat, 2 =medium, and 3 =steep), drainage ditch length, and soil 1646 nitrogen percent. As in the first CCA, we used the same stepwise model building function to 1647 select the key environmental characteristics in the final second CCA; selected variables included 1648 1649 slope intensity, the length of drainage ditches, the average depth to water table, and soil nitrogen 1650 percent. We also quantified unique and shared percentages of variation explained by the competition and environmental variable matrices using variance partitioning. 1651

1652 **Results**

1653 Means and Ranges of Root and Crown Variables

1654 Mean crown extent across all five study species $(2.13 \pm 1.39 \text{ m})$ was found to be

significantly smaller than the mean root system extent $(6.12 \pm 2.15 \text{ m})$ with a ratio of root:crown

- 1656 extent of 2.61 ± 1.11 . The ANOVAs identified a significant effect of species identity on mean
- 1657 crown or root system extent (p-value < 0.01, F-value of 5.4 with 4 degrees of freedom) and
- 1658 compactness (p-value < 0.001, F-value of 5.5 with 4 degrees of freedom). AE had the largest
- 1659 crowns (up to 4.76 ± 0.69 m radius) and longest roots (up to 19.32 ± 4.80 m), and the mean

1660	extent of both crown and roots of AE were significantly greater than those of CO (70% and 90%
1661	of the average, respectively). However, when considering the ratio of root to crown extent, we
1662	found that CO (3.16 \pm 1.44) and HC (2.95 \pm 1.43) had the highest ratios, which were
1663	significantly greater than that of LS (1.95 \pm 0.53). In terms of crown compactness, AE exhibited
1664	the most compact (i.e. homogenously shaped) crowns at the individual tree level (0.54 \pm 0.12),
1665	while HC had significantly less compact crowns (0.38 \pm 0.18). In addition to having the largest
1666	mean diameter at breast height (23 ± 8.0 cm, or 120% of the average), LS had the most compact
1667	root systems, on average (0.73 \pm 0.09), which was significantly more compact than the mean
1668	values of AE (0.46 \pm 0.17), HC (0.47 \pm 0.16), and TR (0.58 \pm 0.24) (Table 1).

1669 The mean Hegyi competition index was lowest for the above-ground neighbourhood 1670 (0.638 ± 0.594) , and highest for the below-ground neighbourhood (2.16 ± 1.20) , which scaled 1671 with focal tree crown and root system size, respectively.

1672 Effects of Competition and Environmental Characteristics on Roots and Crowns

We regressed the natural log of the focal tree biomass against the Hegyi distance-1673 1674 dependent competition index to test which neighbourhoods scale best explained focal tree growth. We calculated the Hegyi competition index using focal and neighbour tree DBH at three 1675 distinct scales: nearest neighbourhood, AGN and BGN. To our surprise, the relationships were 1676 1677 not very significant, perhaps due to scatter in the data, and the strongest relationship was found using the scale of nearest neighbourhood (R^2 of 0.46, Figure 3). The R^2 values for the significant 1678 relationships ranged from 0.04 to 0.46 for BGN and near neighbourhood, respectively, while the 1679 1680 AGN was not found to significantly explain variation in focal tree biomass (p-value of 0.27). Slope values ranged from -0.39 (near neighbourhood) to -0.2 (BGN). In the near neighbourhood 1681

analysis, focal tree biomass varied less from the mean at lower values of the competition indexcompared to higher values.

1684 Plots with AE and LS in the species mixture tended to have larger mean focal tree crown 1685 and root system area. The step forward model selection chose two competition indices, those 1686 calculated at the near neighbourhood and BGN scales. The CCA shows that as competition 1687 intensity increases so too does the plot-level coefficient of variation of root compactness. 1688 Conversely, variation in crown compactness apparently responds more to crown size than to 1689 competition per se (Figure 4). The total amount of variation in root and crown variables 1690 explained in the competition CCA was 66%. The first axis, which explained 47%, was mainly 1691 determined by competition calculated at the near neighbourhood scale, the presence of CO in the species mixture, and competition calculated at the BGN scale (Table 2). The second axis was 1692 primarily explained by the presence of AE, the competition calculated at the BGN, and the 1693 1694 presence of LS, and this axis explained an additional 15% of dependent variable variation.

Plots with more nitrogen-rich soil had focal trees with larger average crown and root 1695 1696 system area. Crown area and compactness variation at the plot level seem to respond to similar 1697 variables, and they exhibited a positive relationship with slope intensity. Greater average depth to water table led to greater variation in root system compactness at the plot level, as well as 1698 somewhat smaller mean root system area (Figure 5). The amount of variation in the dependent 1699 1700 crown and root variables explained by the environmental variables in the CCA was 26%. The first axis, which explained 20% of the variation, was principally determined by soil nitrogen 1701 1702 percent and average depth to water table, and somewhat affected by drainage ditch length, while 1703 the second axis, which explained an additional 5% of variation, was largely determined by slope 1704 intensity, average depth to water table, and soil nitrogen percent (Table 2).

1705 Competition and environmental matrices together explained 76% of the variation in the 1706 crown and root variables. The shared variation explained was 20%, and most of the variation was 1707 uniquely explained by the competition matrix (32%) while the environmental matrix contributed 1708 only 3% uniquely to the variation explained.

1709 **Discussion**

1710 Crown vs. Root System Extent

1711 A small number of studies have reported root:shoot extent ratios for tropical (Ashton, 1975; Malinovski et al., 2015; Sinacore et al., 2017) and temperate trees (Smith, 1964; Tubbs, 1712 1713 1977; Hruska *et al.*, 1999). Climate does not affect this ratio in a clear way, as temperate trees 1714 have been described with both the lowest and highest ratios: Hruska et al. (1999) reported a mean root:shoot extent ratio of 0.6 in a floodplain forest, while Malinovski et al. (2015) depict 6-1715 1716 year old *Eucalpytus grandis* x *urophylla* in a temperate, experimental stand in southern Brazil 1717 with a root:shoot extent ratio of nearly 7. For our first objective, we found that the mean root:crown extent in Sardinilla was 2.61 ± 1.11 , which falls within the range established by 1718 1719 these prior studies. 1720 Competition with neighbours has been shown to reduce root:crown extent ratios of five 1721 temperate species in British Columbia, where this ratio ranged from 1.01 to 2.48 for trees grown

in the open and from only 0.48 to 0.91 for trees grown in forests (Smith, 1964).

In addition to competition with neighbours, focal tree ontogenetic stage is a key factor in determining crown and root system extent. Sinacore *et al.* (2017) fully reconstructed the root systems of 40 trees that were eight years old with destructive sampling and full root system excavation. They harvested trees from the same site in Panamá, as well as from the Soberania site, and our studies shared three species in common, namely AE, CO and TR. At this age, these

species exhibited root:crown extent ratios that ranged from 3.03 ± 0.28 (AE) to 5.49 ± 1.07 (TR) 1728 (and CO had 5.00 ± 0.49); as determined in our study, all three of these species' ratios decreased 1729 1730 over the next eight years of growth, ranging from 2.40 (AE) to 3.16 (CO), despite increases in absolute crown and root extent. In his review of growth of root and shoot development of 1731 1732 *Eucalyptus regnans* (F. Muell.), Ashton (1975) described a similar ontogenetical trend in 1733 Australia. Root extent was greater than crown extent for around the first 60 years of growth, especially between 10 to 20 years of age, where root systems extended up to three times as far as 1734 1735 crowns. Once trees reached maturity at around 60 years of age, the ratio of root:crown extent 1736 approached 1, after which the root and crown extent increased in tandem. Given that the age of the Sardinilla experiment is younger than 20 years, the AE, CO and TR focal trees were clearly 1737 not yet mature; these trees seem to have first prioritized the establishment of a far-reaching root 1738 system, then redistributed their energetic investments into lateral crown growth, likely to 1739 increase their competitive ability. Indeed, Ammer's review of mixture effects and forest 1740 1741 productivity (2019) made the case that young trees first establish below-ground organs to efficiently absorb nutrients and water that subsequently allow increased energetic investment 1742 above-ground for purposes such as expanding crown dimensions or engaging in morphological 1743 1744 plasticity.

The difference in extent of crowns and root systems might be explained by the distinct mechanisms of competition that operate above- and below-ground, i.e. asymmetric versus symmetric competition (Mina *et al.*, 2018; Cahill and Casper, 2000; Casper and Jackson, 1997). Though they did not assess root system extent, Schröter *et al.* (2012) showed that European beech (*Fagus sylvatica* L.) tree crowns tended to be displaced from their respective stems by neighbours up to 12 meters away, and that this morphological plasticity resulted in 10% higher

canopy cover than if trees did not employ this displacement strategy. Root systems may be able
to continue expanding into root gaps, i.e. uncolonized areas of the soil, while crowns are
physically constrained by the branches of nearer neighbours. This proposed difference in space
filling might explain our observation in the neighbourhood CCA that focal trees exhibited more
significantly reduced crown area than root system area when growing near large neighbours.

1756 Neighbourhood Scale

1757 Regarding our objective to understand which of the three neighbourhood extents best explained focal tree biomass, we found an overall weak relationship that was somewhat stronger 1758 1759 for the near neighbourhood. This near neighbourhood extended only 4.5 meters from the focal 1760 trees, which is a smaller effective radius than many studies of neighbourhood effects on focal trees, with the exception of Chi et al. (2017). We suggest that this small neighbourhood radius is 1761 1762 due, in large part, to the relatively young age and somewhat small size of our focal trees (mean 1763 DBH of 19.4 ± 8.4 cm) compared to these other studies. In line with our results, von Oheimb et 1764 al. (2011) found that the best fitting radius to predict biomass was around 5.5 to 6.5 meters for 1765 trees between 16 and 39 years of age. In contrast, Lu et al. (2015) found through preliminary 1766 analysis that a 20-meter radius neighbourhood best represented neighbourhood effects on focal seedlings and Kramer et al. (2019) could predict crown radius and trunk form with 1767 neighbourhoods of 30-meters better than with smaller neighbourhoods. However, it should be 1768 1769 noted that Kramer et al. (2019) only included in their study temperate Picea trees that were 1770 mature and taller than 60 meters, while our trees were much younger. Indeed, such analyses 1771 performed with older and larger trees report much larger neighbourhood extents; Uriarte et al. (2004) found that 12 tropical tree species in Puerto Rico and ranging from 32 cm to 151 cm DBH 1772 responded to neighbours up to 14 meters on average from the focal trees. Similarly, Stoll and 1773

Newbery (2005) reported considerably varied neighbourhood radii, from five to 20 meters, for
10 dipterocarp species between 10 and 100 cm DBH in Malaysia, depending upon the sensitivity
of each species to conspecific and heterospecific neighbours.

1777 Neighbourhood vs. Environmental Characteristics

1778 In addressing our third objective, we found that crown and root system morphology 1779 responded more strongly to competition with neighbours and neighbour identity than to abiotic characteristics. The importance of neighbour tree size and species identity in determining focal 1780 1781 tree crown architecture has a strong foundation in the literature (Brisson, 2001; von Oheimb et 1782 al., 2011; Schröter et al., 2012; Sapijanskas et al., 2014; Jucker et al., 2015; MacFarlane and 1783 Kane, 2017). Valverde-Barrantes et al. (2013) reported similar findings to ours in their study of root trait variation of four species of temperate trees in a 65-year old forest: they were more 1784 significantly affected by focal tree and neighbour species identities than by soil characteristics. 1785 1786 They argued that different tree species may employ distinct below-ground root architecture or phenology, resulting in reduced below-ground competition with neighbouring heterospecific 1787 trees. This has been shown in some studies of fine root placement and phenology (Brassard et 1788 1789 al., 2013; Laclau et al., 2013), though such effects do not manifest in all species assemblages 1790 (Meinen et al., 2009). Furthermore, differences in above-ground architecture between CO, LS 1791 and AE may shed light on their opposing effects on focal tree crowns and root systems: LS and 1792 AE were characterized by having many branches and leaves, likely limiting light interception of the focal trees, while CO grew tall with sparser branches and fewer leaves and thus may not have 1793 been a strong competitor for light. Perhaps focal trees in plots with AE and LS neighbours grew 1794 1795 broader crowns to intercept sufficient light under these neighbours' denser canopies, as MacFarlane and Kane observed for focal trees growing under shady forest conditions (2017). 1796

1797 Their root systems may have grown correspondingly larger to provide physical stability (Ow *et*1798 *al.*, 2010).

1799 In forests with more scarce soil nutrients, local environmental characteristics have been 1800 shown to exert a much more significant effect on focal trees than interactions with neighbour 1801 (Baribault and Kobe, 2011). Furthermore, Putz and Canham (1992) found that seedlings and 1802 neighbouring shrubs engaged in stronger root competition than competition for light in sites of lower soil nutrient and water availability, while the reverse was true in more nutrient-rich sites. 1803 1804 In the Sardinilla experiment, the importance of neighbourhood characteristics may have overshadowed environmental characteristics either because competition with neighbours for 1805 1806 above-ground resources such as light was much more intense than for soil nutrients or because soil nutrients at the plot scale were ample for tree growth requirements; unlike many tropical 1807 forests, phosphorous may not have been a limiting nutrient for growth due to the limestone 1808 1809 parent material and high pH of the site (T. Moore, personal communication, June 14, 2018). 1810 Furthermore, phosphorus was not retained as one of the abiotic variables due to its relatively small explanatory power for root traits compared to nitrogen. However, focal trees were 1811 1812 observed to grow larger crowns and root systems in soil with greater local nitrogen content and 1813 lower mean depth to water table. Perhaps similarly, Mirabel et al. (2019) found that seedling growth rate could be best explained by placing their above- and below-ground traits on efficient-1814 1815 conservative axes of the absorption of soil nutrients and water. Improved drainage and lower 1816 mean depth to water table has been shown to be particularly important during the wet season 1817 (Kunert et al., 2012), necessitating that focal trees utilize smaller crowns and root systems and 1818 exploring the soil for better aerated patches with fewer, longer lateral roots (Madsen *et al.*, in review). 1819

1820 Conclusions

1821 This study uses a dataset that is notable for its inclusion of root systems and crowns of trees planted nearly twenty years ago and measuring up to 24 m in height. With it, we provide 1822 1823 evidence that unifies the frequently separated above- and below-ground compartments of trees, 1824 illustrating that the extent and morphology of tropical trees' crowns and root systems are largely determined by competition intensity and species identity of their nearest neighbours rather than 1825 1826 environmental characteristics. Furthermore, we show that growth rates of young tropical trees 1827 may be best explained with the Hegyi competition index at the simpler and more easily measured 1828 near neighbourhood scale, rather than neighbourhoods determined by the extent of crowns or root systems. This may facilitate forest surveys or simple investigations of competition in young 1829 1830 forest stands by obviating the need for labour-intensive root excavation and LiDAR scanning. 1831 That being said, we cannot claim that such analyses will always be a 'walk in the park', as each species of tree may forage and compete in a different fashion. 1832

1833 **Tables**

1834 Table 1. Mean diameter at breast height (DBH), crown extent and mean root system extent for

1835 pooled data and for all five study species (*Anacardium excelsum (AE)*, *Cedrela odorata (CO)*,

1836 Hura crepitans (HC), Luehea seemannii (LS), and Tabebuia rosea (TR)). Significant differences

are indicated by lower-case letter groupings, where 'a' is different from 'b' but not 'ab.' N = 128focal trees.

Species	Mean DBH (± sd) (cm)	Mean Crown Extent (± sd) (m)	Mean Root System Extent (± sd) (m)	Mean Crown Compactness (± sd)	Mean Root System Compactness (± sd)	Ratio (Root:Crown Extent) (± sd)
Δ 11	$19.37 \pm$	$2.13 \pm$	$6.12 \pm$	0.47 ± 0.18	0.58 ± 0.21	2.61 ± 1.11
	8.39	1.39	2.15			
٨F	$21.3 \pm$	$2.80 \pm$	$7.37 \pm$	0.54 ± 0.12 a	$0.46\pm0.17~b$	2.40 ± 0.69
AL	7.78 ab	1.56 a	2.38 a			ab
CO	19.6 ±	$1.60 \pm$	$5.70 \pm$	0.45 ± 0.19	0.62 ± 0.22	3.16 ± 1.44 a
CO	8.99 ab	1.48 b	2.32 b	ab	ab	
ЧС	$17.3 \pm$	$1.66 \pm$	$5.54 \pm$	$0.38\pm0.18~b$	$0.47\pm0.16~b$	2.95 ±1.43 a
пс	9.44 ab	1.27 ab	1.53 b			
IC	$22.8 \pm$	$2.55 \pm$	$5.62 \pm$	0.48 ± 0.13	0.73 ± 0.09 a	$1.95\pm0.53~b$
LS	7.97 a	1.35 ab	1.87 b	ab		
TD	$15.3 \pm$	$1.88 \pm$	$6.50 \pm$	0.48 ± 0.17	$0.58\pm0.24\ b$	2.66 ± 0.71
IK	5.81b	0.86 ab	2.08 ab	ab		ab

1839

- 1841Table 2. Axis loading factors of independent variables of the competition and environmental
- 1842 canonical correspondence analyses (CCA) for all five study species (*Anacardium excelsum (AE*),
- 1843 Cedrela odorata (CO), Hura crepitans (HC), Luehea seemannii (LS), and Tabebuia rosea (TR)).
- 1844 Hegyi_NN represents the Hegyi competition index calculated at the near neighbourhood and
- 1845 HegyiRoot represents the same but calculated for the below-ground neighbourhood. N = 20
- 1846 plots; the three variables with the highest loading factors for each axis are presented in **bold**.

CCA	Independent Variable	First Axis	Second Axis
(total variation		Loading Factor	Loading Factor
explained)			
	CO	0.59	-0.14
	AE	-0.26	0.49
Competition (65.8%)	LS	-0.24	-0.26
	Hegyi_NN	0.70	0.19
	HegyiRoot	0.39	0.36
	Slope Intensity	-0.026	0.78
Environmentel	Ditch Length	0.27	0.15
(26.0%)	Average Depth to Water Table	-0.41	-0.62
	Soil Nitrogen %	0.47	0.50

1848 Figures

1849



1850

1851 Figure 1. Crown compactness index assigned values near 1 for shapes that more closely

approximated a circular shape (left) while shapes that deviated more from this circular shape

1853 were assigned values < 1 (right).



Figure 2. Example plot illustrating the excavated roots of the focal trees, their neighbours as
yellow dots, and the three neighbourhood scales we compared: near neighbourhood (maximum
of eight live neighbours, green circles of radius ~4.5 m), above-ground neighbourhood
(polygons, coloured according to species identity), and below-ground neighbourhood (circles of
variable radius, coloured according to species identity). Study species include *Anacardium*madaum (AE). Coducts of denote (CO). Huma manifums (UC). Lucker compared: (LS).

excelsum (AE), *Cedrela odorata* (CO), *Hura crepitans* (HC), *Luehea seemannii* (LS), and

- *Tabebuia rosea* (TR); N = 128 focal trees.



1866

Figure 3. Linear regressions that illustrate the dominant, negative effect of larger neighbours in the near neighbourhood (panel "A"; maximum 8 neighbours) as compared to the above-ground neighbourhood (panel "B") and below-ground neighbourhood (panel "C") in the tropical planted

1870 forest of Sardinilla, Panamá. Slope values were -0.39 (A), -0.24 (B), and -0.2 (C). Coloured lines
1871 are simple linear regression fit with standard error represented as grey margins of lines; "p"

1872 refers to p-values. N = 128 focal trees.



Figure 4. Canonical correspondence analysis of competition's effect on four dependent variables
(crown area, root system area, and the coefficient of variation at the plot level of crown
compactness and root system compactness) with independent variables including the Hegyi
competition index calculated at the near neighbourhood scale ("Hegyi_NN")and calculated at the
root neighbourhood scale ("HegyiRoot"), and the presence of AE, LS and CO trees in the plot.
Total variation explained was 65.79%. First axis explained 47.16% of the variation in response
variables and second axis explained an additional 15.18% of the variation. N = 20 plots.



Figure 5. Canonical correspondence analysis of environmental characteristics' effects on four dependent variables (crown area, root system area, and the coefficient of variation at the plot level of crown compactness and root system compactness) with independent variables chosen by forward-step model builder "ordistep" function; these variables include average depth to water table ("AverageWaterTH") (m), the length of drainage ditches (m), soil nitrogen (%), and an index of slope intensity. All variables were calculated at the plot level. Total variation explained was 25.96%, where the first axis explained 20.00% of the variation and the second axis contributed an additional 5.40% to the explained variation. N = 20 plots.

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General Conclusions

In this thesis, I fulfilled my objectives of furthering our understanding of how coarse root 2093 2094 traits vary depending on neighbourhood and environmental characteristics and of connecting tree 2095 crown and root systems in terms of their response to the local biotic and abiotic environment. 2096 Our principal finding was that tree neighbourhoods (neighbour size, species identity) are key to 2097 understanding both crown extent, root system extent and coarse root traits like root length, diameter and branching intensity. Coarse root morphology also responded to abiotic 2098 2099 characteristics: higher soil nitrogen led to longer primary roots with fewer secondary roots, while 2100 trees in seasonally waterlogged soil grew fewer but longer primary roots. Interestingly, we 2101 observed some synergy in how trees responded to certain biotic and abiotic independent 2102 variables, such as how trees growing in soil with deeper average water tables and in 2103 neighbourhoods composed of more conspecifics tended to have more laterally constrained root systems with more lateral roots. We proposed that this may represent a strategy that serves 2104 2105 multiple purposes for tropical trees, reducing competition with neighbours' root systems and also 2106 increasing water absorption in soil with deeper water tables.

We also attempted to link the crowns and root systems of tropical trees by showing that, after accounting for focal tree size, the size, proximity and species identity of neighbour trees were of paramount importance in determining these above- and below-ground systems' extents and morphologies. The biomass of these young trees was best explained by competition rendered at the near neighbourhood scale, as opposed to competition with all trees whose stems were overlapped by either the focal tree crown or root system.

2113 The findings of this thesis may be particularly applicable to scientific studies of tree-tree 2114 competitive interactions. The finding that nearest neighbours best explained focal tree biomass

may facilitate forest surveys or simple investigations of competition in young forest stands by 2115 obviating the need for labour-intensive root excavation and LiDAR scanning. Numerous 2116 2117 questions remain, such as how generalizable these results are for other forest types, ages and soil qualities. Future research could build on our findings by assessing if root-root competition plays 2118 a more dominant role in determining focal tree size at different stand ages; perhaps below-2119 2120 ground competition is of primary importance in younger stands in which canopy closure has not 2121 yet occurred, reducing the intensity of competition for light? 2122 In terms of applicability to industry (e.g. plantations for timber), our findings also suggest 2123 that planting mixtures of tree species may allow the planted trees to develop broader root systems that may allow trees to attain higher growth rates and persist in seasonally waterlogged 2124 2125 conditions, and crowns that are more efficient in terms of light capture, compared to trees 2126 planted in monocultures. Although we found that the tropical tree roots extended in some cases 2127 up to 20 meters from the stem, past work on root and crown extent has suggested that these two 2128 systems indeed reach comparable distances from the stem when trees become mature (Ashton, 1975). Therefore, we do not think it is necessary to plant trees further apart to limit below-2129 2130 ground competition during the mature stage of growth.

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