UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE ECOLOGÍA
ECOLOGÍA

IMPACTO DE UN INGRESO ELEVADO DE N EN SU CICLO Y SUS PÉRDIDAS EN BOSQUES TROPICALES SECOS DE YUCATÁN

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

ANAITZI GABRIELA RIVERO VILLAR

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CIUDAD UNIVERSITARIA, CD.MX., FEBRERO, 2022

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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

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ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 20 de septiembre de 2021 se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **RIVERO VILLAR ANAITZI GABRIELA,** con número de cuenta **514012324,** con la tesis titulada **: "IMPACTO DE UN INGRESO ELEVADO DE N EN SU CICLO Y SUS PÉRDIDAS EN BOSQUES TROPICALES SECOS DE YUCATÁN*",*** bajo la dirección del **DR.HOMERO JULIO EUDES CAMPO ALVES**, Tutor Principal, quedando integrado de la siguiente manera:

Presidente: DR. FELIPE FRANCISCO GARCÍA OLIVA
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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 25 de noviembre de 2021

COORDINADOR DEL PROGRAMA

COORDINACIÓN

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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Sr. José

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Resumen

Existe una gran incertidumbre respecto a cómo responderán los bosques tropicales secos (BTS) a las presiones antropogénicas, siendo de particular interés para esta investigación los cambios en el régimen de lluvias en respuesta al cambio climático global y el aumento de los depósitos de nitrógeno (N) atmosférico. Las evidencias indican que, de no cambiar las prácticas actuales de producción, consumo y uso de recursos, la crisis ambiental se exacerbará. Los modelos climáticos estiman que, para finales de este siglo, las regiones tropicales experimentarán severos cambios en sus regímenes de lluvias, con una tendencia a volverse más secos y con mayor ocurrencia de eventos extremos de sequía. De igual manera se espera que las entradas de nitrógeno reactivo (Nr) por depósito desde la atmósfera puedan incrementarse entre 50 y 100% respecto a sus tasas del año 2000, las cuales ya eran altas como consecuencia del uso desmedido de fertilizantes nitrogenados y la quema de combustibles fósiles, principalmente. Por otra parte, las respuestas de los BTS a estos cambios dependerán de las condiciones biofísicas de cada bosque, particularmente de la fertilidad de sus suelos, por lo cual es imprescindible un análisis de tales condiciones. En el marco de estos dos cambios globales (i.e. en el régimen de lluvias y en el depósito atmosférico de N) y de la necesidad de contar con una actualización de las características de los suelos de este bioma tropical, la presente tesis aborda estos temas prioritarios en tres capítulos, y finalmente aborda una reflexión respecto a las amenazas de estos dos forzadores del cambio funcional en estos ecosistemas.

En el primer capítulo se presenta una revisión de las generalidades edáficas del bioma a escala pantropical, que nos permitió comprender cuáles son los principales tipos suelos y sus características hidrológicas y químicas de los BTS. Además, se explora la relación de estas características con el clima, lo cual ha permitido establecer una línea base de la biogeoquímica de los suelos de estos bosques. Los resultados sugieren que los almacenes de carbono (C), nitrógeno (N) y fósforo (P) son sensibles a la aridez, y ante las tendencias globales de disminución de la precipitación y aumento de la temperatura, estos bosques pondrían convertirse en fuentes netas de C y N a la atmósfera, teniendo una retroalimentación positiva en el clima global exacerbando así el calentamiento global.

En el segundo y en el tercer capítulo se presentan estudios experimentales que evalúan la dinámica del ciclo del N realizados en los BTS de Yucatán. En el segundo capítulo se explora la variabilidad natural del ciclo del N bajo condiciones contrastantes del régimen de lluvias, mientras que en el tercero se evalúan las variaciones en el ciclo del N en respuesta a la interacción de los cambios en el

régimen de lluvias y el aumento en el depósito de N acorde con las tasas esperadas para el año 2030 en la región tropical. Para llevar a cabo los experimentos en campo se seleccionaron dos BTS maduros con diferente cantidad de lluvia anual; el sitio subhúmedo recibe 1240 mm año^{-1} mientras que el semiárido 642 mm año^{-1}. El resto de las características biofísicas son similares (i.e. la altitud, temperatura media del aire, el material parental y el tipo de vegetación), lo cual permitió sugerir que los cambios en el ciclo de N fuesen atribuidos a las diferencias en el régimen de precipitación, y su sinergia con los aumentos en los depósitos atmosféricos de N esperados para la región en cuestión.

Ambos estudios muestran el fuerte efecto que ejerce el régimen de lluvias en las tasa y patrones del ciclo de N en los bosques estudiados. Las evidencias indican que el ciclo de N es más abierto conforme las condiciones de disponibilidad de agua son menores, esto se infiere principalmente a través de marcar la abundancia natural de $\delta^{15}N$ en el suelo y la vegetación; el mayor enriquecimiento de ^{15}N observado en el sitio semiárido sugiere un menor control del ciclo interno, con mayores pérdidas de N (Capítulo 2). Esto fue corroborado con los resultados obtenidos al evaluar los flujos de óxido nitroso (N_2O), los cuales indican que el sito semiárido presenta el doble de emisiones de N_2O respecto al sitio subhúmedo (Capítulo 3). El experimento de adición de N indica que, tras 10 años de adición experimental de N de forma crónica, el sitio semiárido demuestra una mayor sensibilidad a los cambios en el ingreso del nutriente exacerbando las pérdidas de N hacia la atmósfera, así como por lixiviación, ambos indicadores de un incremento en la apertura de su ciclo. Los resultados refuerzan las evidencias de que el ciclo de N en estos bosques está fuertemente controlado por la disponibilidad de agua.

En general los resultados del trabajo indican la gran sensibilidad de los BTS ante cambios en el régimen de precipitación y conforme aumenten las condiciones de aridez, los ecosistemas en cuestión podrían dejar de ser sumideros de N, incrementando así las emisiones a la atmósfera. Y estas respuestas se verán incrementadas con las nuevas entradas de Nr a los ecosistemas, produciendo así una retroalimentación positiva con el cambio climático global. Finalmente, se reflexiona respecto a las nuevas líneas experimentales de investigación a desarrollar en este importante ecosistema dada su masiva participación en los ciclos globales de carbono y nitrógeno.

Abstract

There is significant uncertainty about how tropical dry forests (TDF) will respond to the imminent anthropogenic pressures, being of this thesis understand the changes in the rainfall regimen in response to global climatic change and the increase in nitrogen (N) deposition. The evidence indicates that if current production, consumption, and use of resources remain as business as usual, they will exacerbate the environmental crisis. The climatic models estimate that tropical regions will experience severe changes in their rainfall patterns by the end of this century, tending to be drier with a more frequent occurrence of extreme drought events. An increase of 50 to 100% of reactive nitrogen (Nr) deposition from the atmosphere is also expected relative to their rates in 2000, which were already were high mainly due to the excessive use of nitrogen fertilizers and burning of fossil fuels. On the other hand, the responses of the TDF to these changes will depend on the biophysical conditions of each forest, particularly on the fertility of their soils, a reason why it is crucial to study them. In the framework of these two global changes (i.e., rainfall regime and the atmospheric N deposition) and the need to update the characteristics of the soils of this tropical biome, this thesis addresses these priority issues in three chapters. Finally, it reflects on the threats of these two forces' functional change in these ecosystems.

The first chapter reviews the edaphic generalities of the TDF on a pantropical scale, which allowed us to understand better the main soil types and their hydrological and chemical characteristics. Also, we analyzed the relationship of these characteristics with the climatic factors, which allowed us to establish the baseline of the biogeochemistry of these forests' soils. The results suggest that carbon (C), nitrogen (N), and phosphorus (P) pool are sensitive to aridity and to the expected global climate changes as is expected (rainfall decreases and temperature increases). In that case, this forest could become a net source of C and N to the atmosphere, with positive feedback aggravating the global climate.

The second and third chapters are an experimental study carried out in the TDF of Yucatán. The second chapter explores the natural variability of the N cycle under contrasting conditions of the rainfall regime. The third chapter evaluates the variations in the N cycle in response to the changes in the rainfall regime and the increase of the N deposition according to the rates expected for the year 2030 in the tropical region. To carry out the field experiments, we selected two mature TDF that differ primarily in the amount of annual rainfall received; the subhumid site receives 1240 mm year-1 while

the semiarid site receives 642 mm year-1. The rest of the biophysical characteristics are similar (i.e., the altitude, mean air temperature, the parental material, and the type of vegetation), allowing us to attribute the differences in the N cycle to the differences in the rainfall regimen and the increases of the atmospheric N deposition.

Both studies show the strong effect of the rainfall regime on the rates and patterns of the N cycle in these forests. The evidence indicates that the N cycle is more open as the water availability decrease, this is inferred mainly through labeling the natural abundance of $\delta^{15}N$ in the soil and vegetation; the greater ^{15}N enrichment observed in the semiarid site suggests less control of the internal cycle, with greater losses of N (Chapter 2). This was corroborated with the results of the nitrous oxide (N_2O) fluxes, which indicate that the semiarid site presents twice the N_2O emissions compared to the subhumid site (Chapter 3). The N addition experiment suggests that, after ten years of chronical N addition, the semiarid site appears to be more sensitive to changes in nutrient inputs, exacerbating N losses to the atmosphere as well as by leaching, which indicates an increase in the opening of its cycle. The results reinforce the evidence that the N cycle in these forests is strongly controlled by water availability.

In general, the results of this study indicate the great sensitivity of the TDF to changes in the precipitation regime; as aridity conditions increase, this forest could be a source of N, thus increasing emissions to the atmosphere. And these responses will be increased with the new Nr inputs to ecosystems, thus producing positive feedback aggravating global climate change. Finally, we reflect on the latest experimental lines of research that should be developed in this critical ecosystem, given its massive participation in global carbon and nitrogen cycles.

Introducción general

Los bosques tropicales son uno de ecosistemas más importantes del mundo. Más allá de la alta diversidad de especies que albergan, tienen un papel preponderante en la biogeoquímica global (Townsend et al. 2011). Si bien estos bosques solo representan alrededor del 12% de la superficie de los ecosistemas terrestres, intercambian más agua y energía con la atmósfera que cualquier otro bioma (Foley et al. 2003), desempeñando así un papel fundamental en la regulación y dinámica del clima regional y global (Siyum, 2020).

Debido a su alta productividad (responsables de cerca del 40% de la productividad primaria neta global) son un importante sumidero de carbono (C), globalmente se estima que ~70% del C bruto se encuentra en bosques tropicales, gran parte de este C está almacenado en la biomasa viva y el suelo (56 y 32% respectivamente) en contraste con los bosques boreales que almacenan más C en el suelo que en la biomasa viva (60 y 20 % respectivamente) (Pan et al., 2011). Además de su importancia en cuanto al ciclo del C, los bosques tropicales tienen una importante contribución al ciclo natural del nitrógeno (N), siendo responsables del 70% de su fijación biológica en ecosistemas terrestres y de poco más del 60% de las emisiones de óxido nitroso (N_2O) hacia la atmósfera (Bai et al., 2012; Tian et al., 2019; Townsend et al., 2011). Las altas tasas de fijación responden a la gran heterogeneidad biogeoquímica del bioma, a escalas tanto espaciales como temporales, lo cual genera que existan zonas de baja y alta disponibilidad de N en regiones relativamente pequeñas (Townsend et al., 2008; Hedin et al., 2009; Menge & Levin, 2017).

Gran parte del conocimiento de los bosques tropicales se ha fundamentado en estudios realizados en las regiones más húmedas; históricamente, los bosques tropicales secos (BTS) han recibido menos atención por parte de la comunidad científica pese a constituir cerca del 40% de la superficie de los bosques tropicales (Sunderland et al. 2015; Powers et al. 2018). Actualmente, la importancia de los BTS empieza a ser más reconocida, y el número de investigaciones en este ecosistema ha aumentado en las últimas décadas. Particularmente, los trabajos de Bullock et al., 1995, Pennington et al., Dirzo et al., 2011 y Bhadouria et al., 2019 son ejemplo de los grandes esfuerzos por caracterizar estos ecosistemas, estas síntesis abordan diferentes aspectos fundamentales de la ecología de los BTS, que va desde la descripción de características climáticas, distribución, diversidad, composiciones florísticas, aspectos generales de su biogeoquímica, los impactos humanos, hasta su conservación y restauración. Lo cual ha permitido mejorar el conocimiento del bioma, no obstante, aún queda mucho trabajo para atender los vacíos existentes.

Particularmente encontramos que existen dos grandes huecos en su conocimiento, (1) descripción edáfica global; (2) mejorar el entendimiento de cómo estos bosques responderán a las presiones derivadas del cambio climático global (i.e. cambios en el régimen de precipitación, aumento de los depósitos atmosféricos de N). Dada su amplia cobertura e importancia ecológica por el papel que desempeñan ante la regulación climática global, resulta prioritario afinar el conocimiento de su funcionamiento ecológico enfatizando las condiciones cambiantes, que permitirán establecer estrategias de conservación efectivas.

Distribución y estado de conservación del bosque tropical seco

Los bosques tropicales secos tienen un rango de distribución delimitado a zonas con una temperatura media anual mayor a 17 ºC, precipitación media anual entre 250 a 2000 mm, con un relación anual de evapotranspiración potencial a precipitación >1 y una marcada estación seca que puede ser de 4 a 6 meses durante los cuales la precipitación es menor a 100 mm mensuales, mientras que cerca del 80% de la precipitación ocurre en la estación de lluvias. Este conjunto de características favorece la distintiva fenología de las plantas (es decir la predominancia de especies caducifolias) y del bosque en su conjunto (Murphy and Lugo 1986; Sánchez-Azofeifa et al. 2005; Dirzo et al. 2011).

Alrededor del 38% de los BTS del Neotrópico se encuentra en México, lo cual representa aproximadamente el 11.7% de la superficie terrestre del país (Challenger y Soberón 2008). Estos bosques se distribuyen a lo largo de la vertiente del Pacífico en una franja casi continua, desde el sur de Sonora (límite más norteño de la distribución global) hasta Chiapas; por la vertiente del Golfo su distribución es discontinua en Tamaulipas y Veracruz, y de forma extensa en la parte noreste de la Península de Yucatán (Miles et al. 2006, Challenger y Soberón 2008).

De forma sistemática, los BTS han estado sujetos a múltiples presiones humanas (Figura 1). Dada su ubicación y accesibilidad han propiciado históricamente el establecimiento de comunidades en la región lo que ha tenido gran un impacto y una destrucción generalizada (Pennington et al., 2018) provocando la disminución de su cobertura original, actualmente este ecosistema es un mosaico de bosques en diferentes estados sucesionales (Quesada et al., 2009). A nivel mundial, casi el 49% de los BTS ha visto transformado su uso a agrícola y/o pecuario principalmente (Portillo-Quintero y Sánchez-Azofeifa, 2010;Stan & Sanchez-Azofeifa, 2019). En América Latina, menos del 10% permanecen intactos, quizá su severa transformación se debe a que se tiene la concepción de que estos bosques se desarrollan sobre suelos fértiles (Pennington et al., 2018). En México más del 70% ha sido convertido a uso tanto agrícola como ganadero, y solo el 0.2% está bajo protección (Portillo-Quintero y Sánchez-Azofeifa, 2010).

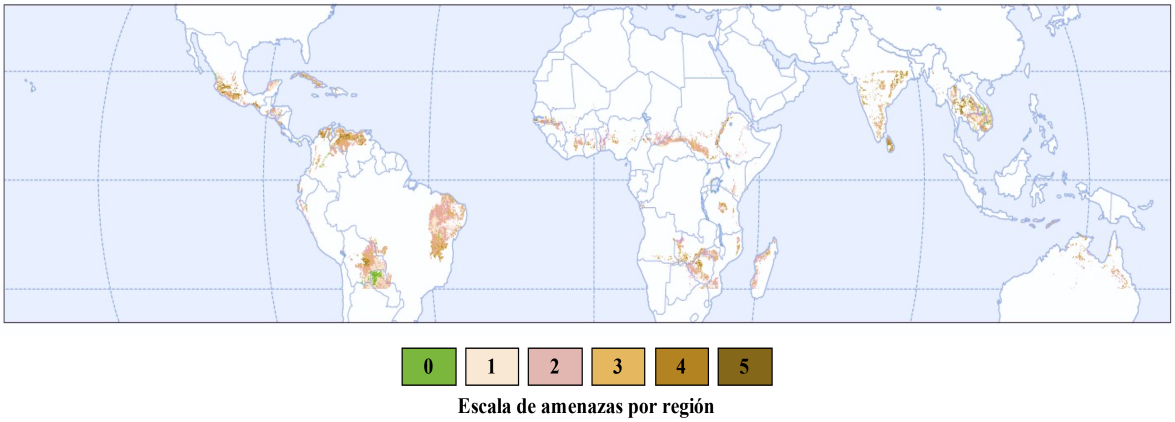


Figura 1. Distribución global de los bosques tropicales secos que ilustra la variación espacial en la exposición a diferentes amenazas. Más del 95% de los bosques están sometido a dos o más amenazas (i.e. cambio climático, fragmentación del bosque, incendios, conversión a agricultura, población humana). El color verde indica las regiones que no están sometidas a alguna de las amenazas mencionadas; en escala de color café se señalizan las regiones que presentan desde una a cinco presiones simultáneamente. Figura tomada y editada de Miles y colaboradores (2006).

En general, los BTS enfrentan eventos inducidos tanto por factores antropogénicos como naturales, que en conjunto con los cambios globales (i.e. cambio climático, aumento de N biodisponible, entre otros) comprometen su capacidad para la adaptación y mitigación al cambio climático (Djoudi et al. 2015; Sunderland et al. 2015). Sin embargo, aún se desconoce la magnitud y dirección de la respuesta de estos ecosistemas ante dichos cambios. Como ya se mencionó, resulta preponderante aumentar los esfuerzos de investigación en estos ecosistemas para tener una mayor certeza de la dinámica ecológica en los BTS a múltiples escalas, incluyendo la dinámica de nutrientes en estos bosques, y así poder predecir las respuestas de cómo responderán a futuras presiones.

Ciclos biogeoquímicos en ecosistemas terrestres

La vida y el óptimo funcionamiento de los ecosistemas depende del suministro adecuado y balanceado de elementos (Lavelle et al., 2005). Los cuales quedan biodisponibles y circulan por los compartimientos de los ecosistemas a través de un conjunto de procesos controlados por diversos factores (climáticos, edáficos y bióticos), que en su conjunto conforman los ciclos biogeoquímicos (Schlesinger & Bernhardt, 2020). Particularmente los suelos desempeñan un papel fundamental para los ciclos biogeoquímicos, ya que gran parte de los procesos de transformación de los nutrientes ocurren en la matriz del suelo. Los suelos son un determinante principal de la calidad del sitio y las condiciones ambientales en los ecosistemas terrestres, proporcionando agua, nutrientes, refugio y anclaje para las formas de vida terrestres (Cronan, 2018). Es por ello que se considera que el suelo juega un papel fundamental en la prestación de múltiples servicios ecosistémicos (Smith et al., 2015) entre los que destacan los ciclos biogeoquímicos.

De forma simplista y genérica los ciclos biogeoquímicos describen el movimiento de nutrientes dentro y entre las diversas entidades bióticas (microrganismos, plantas y consumidores) y abióticas (matriz del suelo, atmósfera) a través del ecosistema y entre ecosistemas. Los nutrientes entran a los ecosistemas mediante la meteorización química de la roca, el transporte lateral, la fijación biológica, el depósito húmedo y seco de nutrientes que se encuentran suspendidos en la atmósfera, o por el reciclaje de sus formas orgánicas (descomposición de la materia orgánica) convirtiéndolos a la forma iónica, lo que permitirá su absorción temporal por parte de la biota y su futuro retorno al suelo o a la atmósfera. Mientras que las principales formas en las que salen es a través de la lixiviación, la emisión de gases, la erosión eólica e hídrica y los incendios, completando así la circulación de los nutrientes por todos los compartimentos de los ecosistemas (Lavelle et al., 2005; Vitousek & Matson, 2009; Chapin III et al., 2011; Cronan, 2018; Schlesinger & Bernhardt, 2020;).

En condiciones de estabilidad, los ecosistemas tienden a mantener sistemas relativamente cerrados con ciclos conservativos de nutrientes, es decir donde las entradas y salidas de nutrientes hacia o desde los ecosistemas corresponden a una pequeña fracción de la cantidad de nutrientes que circulan internamente. Sin embargo, las presiones antropogénicas han tendido a incrementar las entradas y salidas en relación con las transferencias internas generando que los ciclos de los elementos sean más abiertos (Chapin III et al., 2011).

Ciclo del nitrógeno en ecosistemas terrestres

El nitrógeno en su forma molecular (N_2) es el gas más abundante de la atmósfera terrestre (~79%), y es el cuarto elemento más abundante en la biomasa celular (Stein & Klotz, 2016). Este elemento es esencial para cualquier forma de vida, dado que es utilizado para la síntesis de los ácidos nucleicos y las proteínas. Pese a su gran abundancia en la atmósfera, el N_2 es prácticamente inerte, por lo tanto, no está disponible para la gran mayoría de organismos, mientras que en algunos ecosistemas el N fijado en iones de nitrato (NO_3^-) y anónimo (NH_4^+) a menudo no es suficiente, limitando así la productividad primaria de estos (Elser et al., 2007; Canfield et al., 2010; Robertson & Groffman, 2015).

La biogeoquímica del N depende casi por completo de reacciones de reducción-oxidación principalmente mediadas por la comunidad microbiana el suelo, y en menor grado en el reciclaje a largo plazo a través de la geósfera (Canfield et al., 2010; Thamdrup, 2012). En el diagrama de la (Figura 2), se ilustran las vías y procesos primarios mediante los cuales los microrganismos participan en el ciclo de N en ecosistemas terrestres.

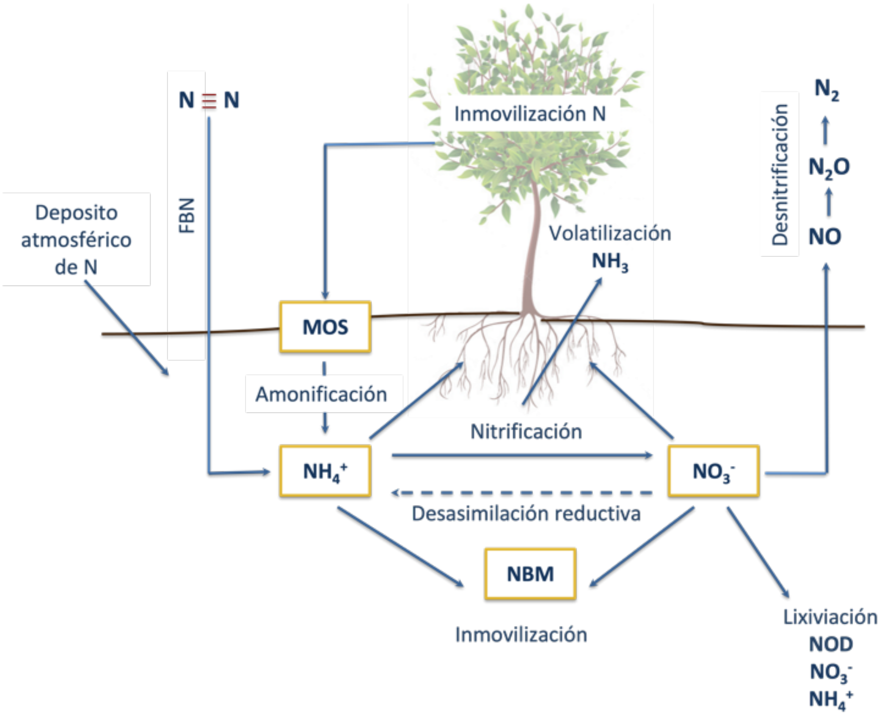
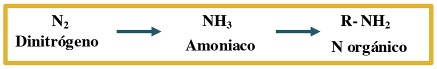


Figura 2. Descripción simplificada de las vías del ciclo del nitrógeno en ecosistemas terrestres (Modificado de Chapin III et al., 2011). FBN, fijación biológica de nitrógeno; MOS, materia orgánica del suelo; NBM, nitrógeno en biomasa microbiana.

En términos generales el ciclo del N se puede simplificar en los siguientes pasos:

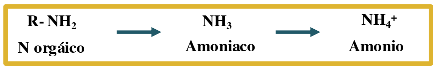
- La **fijación biológica de nitrógeno (FBN)** implica la transformación de N_2 a N orgánico, siendo esta la principal vía natural mediante la cual el N ingresa a las reservas del suelo. La FBN es un proceso restringido a un grupo limitado de procariotas (arqueas y bacterias) de vida libre o simbióticas. Si bien existe un número limitado de especies bacterianas que fijan N_2, representan una amplia variedad de tipos filogenética y fisiológicamente distintos, que se caracterizan por tener la maquinaria enzimática (nitrogenasa) indispensable para cataliza la reducción del N_2 a NH_3 para posteriormente incorporar el N a las estructuras celulares (nitrógeno orgánico $R\text{-}NH_2$). La nitrogensas es extremadamente sensible a su desnaturalización al estar en presencia de oxígeno (O_2), razón por la cual las bacterias fijadoras de N aeróbicas han desarrollado varios mecanismos para protegerla. El proceso de fijar N demanda gran cantidad de energía, por lo cual ocurre únicamente cuando la bacteria tiene un suministro de carbohidratos y fósforo adecuado, problema que algunas especies como *Rizobium*, *Frankia* entre otros grupos lo han solventado al establecer asociaciones simbióticas con plantas como las leguminosas.



- El **depósito atmosférico de N** se refiere al N que entra en forma de partículas disueltas y gaseosas, si bien todos los ecosistemas reciben aportes de N desde la atmósfera, representa una pequeña fracción de las entradas de N, las cuales se han visto incrementadas a consecuencia de las actividades antropocéntricas.

- Durante la **descomposición de la materia orgánica (MO)** los microrganismos y otros organismos del suelo degradan la materia orgánica, los microorganismos mediante la acción de exoenzimas liberan N orgánico disuelto (NOD) como subproductos del consumo de la MO. Las plantas y los hongos micorrízicos absorben parte del NOD y lo utilizan para apoyar su crecimiento. Los microrganismos descomponedores también utilizan parte del NOD para sus requerimientos de N y C durante su crecimiento.

- **Mineralización** o también llamada **amonificación**, es la conversión de N orgánico a formas inorgánicas. Este proceso es llevado a cabo por un amplio conjunto de microrganismos que descomponen el NOD, y utilizan el esqueleto de C como fuente de energía y secretan NH_4^+ a la solución del suelo. Si la MO de las plantas es rica en N, las necesidades microbianas se satisfacen fácilmente y se produce la liberación de N (mineralización), de lo contrario los microbios deben inmovilizar el N inorgánico. Por lo tanto, la calidad de la MO es la que determina el balance entre estos procesos.



- La **nitrificación** es la oxidación microbiana del NH_4^+, implica la transformación parcial o total del NH_4^+ a formas menos reducidas. Durante este proceso el NH_4^+ es oxidado a nitrito (NO_2^-) y subsecuentemente a NO_3^-. Este proceso es realizado por un grupo restringido de bacterias nitrificantes que pueden ser tanto heterótrofas como autótrofas, estas últimas utilizan la energía de la oxidación del NH_4^+ para fijar C. La nitrificación también puede ser fuente directa e importante de gases atmosféricos NO_x y N_2O a través de la desnitrificación cuando la cantidad de O_2 es bajo o mediante la formación de subproductos. Los principales reguladores de la nitrificación son la disponibilidad de amonio en el suelo, y la disponibilidad de O_2, ya que todos los nitrificantes conocidos son aerobios obligados, y la nitrificación avanza muy lentamente, si es que ocurre, en suelos anegados.

- La **reducción desasimilatoria de nitrato a amonio** se refiere a la transformación anaeróbica de NO_3^- a NO_2^- y luego a NH_4^+. Este proceso permite que la respiración continúe en ausencia de O_2 y se cree que se ve favorecida en ambientes donde la proporción de C a NO_3^- es alta dado que es un proceso que consume muchos electrones. Se ha encontrado que es común e importante en algunos suelos de bosques tropicales.

- La **inmovilización** implica la remoción temporal de N inorgánico disponible del suelo, por parte de la biota, mediante absorción y fijación química.

- La **desnitrificación** es la reducción de NO_3^- a formas gaseosas de N, como óxido nítrico (NO), óxido nitroso (N_2O) y dinitrógeno, ocurre cuando el suelo está saturado de agua y el O_2 no está disponible y las bacterias usan el NO_3^- como fuente de oxígeno. Este proceso es conducido por una amplia variedad de bacterias, en su mayoría heterótrofas, que utilizan el NO_3^- en lugar del O_2 como aceptor de electrones durante la respiración.

- La **volatilización de amoniaco** junto con la nitrificación y desnitrificación son las principales vías de pérdida de N en forma gaseosa. Los flujos de gas están controlados por las características del suelo y ambientales que regulan las tasas de difusión a través de los suelos.

$$\boxed{\underset{\text{Amonio}}{NH_4^+} \longrightarrow \underset{\text{Amoniaco}}{NH_3}}$$

- La **lixiviación** es el mecanismo por el cual se pierde N del ecosistema, tanto en su forma orgánica como inorgánica que se encuentren en la solución del suelo.

Dado que el ciclo del N es fuertemente mediado por la comunidad microbiana del suelo, las condiciones abióticas del suelo (humedad, temperatura, saturación de O_2, textura) así como la cantidad y calidad de los insumos serán los principales factores que controlan las tasas y patrones de este ciclo (Vitousek & Matson, 2009; Thamdrup, 2012; Bottomley & Myrold, 2015; Robertson & Groffman, 2015; Stein & Klotz, 2016;). Es por ello que a escala de biomas se puede observar que los proceso biogeoquímicos guardan ciertos patrones similares pese la heterogeneidad intrínseca, la cual indica la variación dentro del bioma en los procesos a través de múltiples escalas espaciales y temporales (Waring et al., 2021).

La biogeoquímica de los bosques tropicales secos

En general, los BTS presentan una gran heterogeneidad biogeoquímica, que refleja la pronunciada variabilidad de las propiedades edáficas, climáticas y bióticas como generalmente ocurre en las regiones tropicales (Townsend et al., 2008; Waring et al., 2021). Al igual que con otros ecosistemas áridos y semiáridos, la frecuencia y la magnitud de los eventos de precipitación ejercen un control directo en la disponibilidad de agua del suelo, que a su vez controlan muchas funciones y servicios de los ecosistemas. Múltiples estudios han corroborado que la disponibilidad de agua suele ser el principal factor que controla la productividad primaria neta, y determina los patrones y procesos de los ciclo biogeoquímicos (Austin et al., 2004; Dirzo et al., 2011; Powers et al., 2018; Campo & Merino, 2019; Castro et al., 2018; Calvo-Rodriguez et al., 2020).

La disponibilidad relativa de los nutrientes en el suelo se ve fuertemente influenciada por las condiciones del régimen de lluvias de cada bosque, siendo más importante la magnitud de los eventos de lluvia individuales o la variabilidad interanual, que el total anual (Knapp et al., 2015). En general, la dinámica de los ciclos de nutrientes en estos ecosistemas estacionales se encuentra claramente diferenciada entre los procesos que ocurren durante la estación de lluvias respecto a la estación seca.

Durante la estación seca se acumulan los nutrientes tanto en formas orgánicas como inorgánicas en el suelo (orgánico y mineral). Como consecuencia de la disminución de la actividad microbiana y de las plantas en respuesta al déficit hídrico (Solís & Campo, 2004) y a que gran parte de la vegetación son especies caducifolias que pierden las hojas en esa temporada. Mientras que, durante la estación de lluvias, ocurren la liberación pulsada de estos nutrientes, como resultado de su mineralización (Jaramillo et al., 2011). Durante esta ventana de tiempo es cuando los microrganismos del suelo y la comunidad vegetal son más activos y aumentan su productividad.

La intensidad y la duración de la temporada seca influye fuertemente en la variabilidad interanual en el ciclo de nutrientes, lo que a su vez puede afectar la retención y pérdida de nutrientes a escala del ecosistema (Calvo-Rodriguez et al., 2020; Waring et al., 2021). Regímenes de lluvias atípicos, pueden generar cambios temporales en la dinámica biogeoquímica, potencialmente como respuesta al desacoplamiento entre la disponibilidad de nutrientes durante el tiempo de crecimiento de la biomasa ocasionando cambios en la productividad forestal y la respiración del ecosistema, haciendo que un ecosistema cambie temporalmente de ser sumidero a fuente de nutrientes (Castro et al., 2018; O'Connell et al., 2018; Calvo-Rodriguez et al., 2020). A través del proceso de captura y almacenamiento de carbono, los bosques secos pueden ayudar a mitigar los procesos asociados con el cambio climático (Sunderland et al., 2015).

Ciclos de nutrientes en los bosques tropicales secos de la Península de Yucatán

Trabajos previos han permitido caracterizar algunos de los rasgos funcionales de los BTS de la Península de Yucatán. En general los resultados indican que el gradiente natural de lluvias de la Península, en conjunto con la marcada estacionalidad climática son un factor muy importante para la regulación de diversas funciones ecosistémicas, que en cuestión de nutrientes se refleja en la gran heterogeneidad en la disponibilidad de estos, tanto local como regionalmente, ya que esta variabilidad hídrica incide directamente en las tasas de transformación de estos nutrientes (Bejarano et al., 2014a; Bejarano et al., 2014b; Campo & Merino, 2016).

De forma sucinta los resultados indican que, la concentración de C total y N total e inorgánico en el suelo son mayores en las regiones más secas (Roa-Fuentes et al., 2012; Bejarano et al., 2014b). Mientras que la tasa de mineralización neta de N son mayores en los sitios más húmedos (Roa-Fuentes et al., 2012). La vegetación ha desarrollado diversas adaptaciones en respuesta a la variación en régimen anual de lluvia, en los sitios más secos la densidad de árboles por hectárea es menor, y los árboles son significativamente menos altos que en la contraparte húmeda. En las regiones de alta disponibilidad de agua hay una mayor asignación de biomasa a los tallos, en contraste los árboles de la condición opuesta asigna más biomasa a las raíces finas (Roa-Fuentes et al., 2012). El área foliar específica es mayor en los sitios más húmedos, sin embargo, la concentración de N y P por unidad de masa es menor en contraste a los sitios más secos (Roa-Fuentes et al., 2015).

En forma general la productividad primaria de estos ecosistemas se encuentran limitados por N y P dependiendo el estado sucesional (Campo & Vázquez-Yanes, 2004; Solís & Campo, 2004), esta limitación se encuentra relacionada con la limitación del agua, ya que su baja disponibilidad afecta la absorción de nutrientes disponibles en el suelo, y afecta la liberación y mineralización de nutrientes debida a las bajas tasas de descomposición (Saynes et al., 2005; Bejarano, Crosby, et al., 2014; Campo, 2016). La producción de hojarasca también disminuye aproximadamente 10% en el extremo más seco del gradiente, mientras que la eficiencia en el uso de nutrientes aumenta en entre 20 y 40% para el N y el P respectivamente. La diferencia entre los tiempos de renovación de N y P en el suelo y en la materia orgánica indica que diferentes nutrientes controlan la función del ecosistema a lo largo de este gradiente. Con un patrón de limitación que va de P a N conforme decrece el régimen de lluvia (Campo, 2016).

Se sugiere que las consecuencias a largo plazo de la disminución esperada en el régimen de lluvias en las regiones tropicales secas cambiarían el suministro de N y P teniendo así efectos negativos a largo plazo sobre la productividad primaria y el almacenamiento futuro de carbono de estos bosques (Campo, 2016).

Impacto de los cambios globales en la dinámica de los bosques tropicales secos

Actualmente, las evidencias de las presiones antropogénicas sobre el sistema terrestre, particularmente las que se relacionan con el cambio climático son irrefutables (IPCC, 2021). Dada la urgente necesidad de establecer nuevos paradigmas que integren el desarrollo continuo de las sociedades humanas y el mantenimiento del planeta en un estado resiliente, Rockström y colaboradores (2009), establecieron nueve límites planetarios que deben de ser considerados y cuantificados para lograr el objetivo de que el planeta permanezca dentro de un espacio operativo seguro.

Los flujos biogeoquímicos y el cambio climático son parte de los límites establecidos. Particularmente, el flujo de N es uno de los límites planetarios del cual ya hemos transgredido su umbral seguro, y al ser una variable lenta que interactúa con otros impulsores del cambio global (elevación de gases con efecto invernadero, calentamiento terrestre, alteración de los regímenes de precipitación) tiene la capacidad de regular y amortiguar los cambios y así incidir en la resiliencia del planeta, por tanto tiene un impacto directo en el cambio climático, que es otro de los límites que estamos cercanos a sobrepasar (Rockström et al., 2009; Steffen et al., 2015).

Globalmente, el depósito atmosférico de N reactivo (Nr) que son todas las formas biológicamente activas en la biósfera y fotoquímicamente reactivas en la atmósfera se ha incrementado en un factor de 10 desde la época preindustrial (Galloway et al., 2008; Gruber y Galloway, 2008). Los modelos estiman que para el 2030 las nuevas entradas de Nr a escala global podrían superar entre 50 y 100% de los depósitos respecto a los registrados en los inicios del siglo (Reay et al., 2008). Particularmente para la región tropical, se estima que la tasa de depósito de Nr podría alcanzar ~ 32 kg N ha año^{-1} para el año 2030 (Dentener et al., 2006) y para finales 2100 el aumento podría llegar a los 50 kg N ha año^{-1} (Lamarque et al., 2005). Gran parte de los aumentos ocurre en las regiones tropicales, y como ya se mencionó, en esta región es donde más N circula de forma natural (Tian et al., 2019). Por lo que resulta esperable que el umbral de saturación de N se alcance más rápido respecto a zonas limitadas por este nutriente, como es el caso de los bosques templados (Hietz et al., 2011). Por lo tanto, sería de esperar que el N excedente salga de los ecosistemas vía lixiviación y/o emisión de óxidos de N, incrementando así las tasas naturales de pérdida de N (de Vries y Schulte-Uebbing 2019).

La perturbación humana al ciclo natural del N ha sido consecuencia del uso desmedido de fertilizantes sintéticos, y del depósito de N resultante de la agricultura y la quema de combustibles fósiles. Siendo estos los principales factores del aumento de N_2O atmosférico, que acorde a las últimas estimaciones ha aumentado 0.031± 0.0005 partes por millón (ppm) equivalente a un aumento del 10% entre 1980 y 2019 (Tian et al., 2020; IPCC, 2021). El aumento de este gas con efecto invernadero es preocupante, ya que puede permanecer fotoquímicamente reactivos en la atmósfera más de 100 años, que es un periodo aún mayor que del dióxido de carbono (CO_2). Esto implica que pasará más de un siglo antes de que las abundancias atmosféricas se estabilicen después de la estabilización de las emisiones globales (IPCC, 2021). El aumento del N_2O atmosférico, no solo es alarmante por su contribución al forzamiento radiativo antropogénico, sino que el N_2O también está involucrado en la pérdida de ozono estratosférico (Ravishankara et al., 2009; Fleming et al., 2011; Wang et al., 2014).

En general, tres de los principales gases con efecto invernadero (CO_2, metano (CH_4) y el N_2O) han alcanzado las concentraciones atmosféricas más altas que en cualquiera de los últimos 800,000 años; en 2019 alcanzaron 409.9 ppm de CO_2, 1.9 ppm de CH_4 y 0.33 ppm de N_2O, lo que corresponde a aumentos de alrededor del 47%, 156% y 23%, respectivamente, por encima de los niveles del año 1750 (IPCC, 2021). Indiscutiblemente los niveles se han alcanzado como consecuencia de las actividades antropogénicas que han roto el balance natural de los ciclos biogeoquímicos. Gran parte de las contribuciones de estos gases con efecto invernadero son emitidas en las regiones tropicales.
A escala global, el cambio climático no solo ha alterado el régimen de lluvias anual, sino también su distribución estacional y variabilidad interanual. Sin embargo, los cambios en los regímenes de lluvias serán mayores en las regiones áridas y semiáridas donde la disponibilidad de agua, tanto en cantidad como en temporalidad, son factores clave que controlan los ciclos biogeoquímicos, la productividad primaria, la fenología del crecimiento entre otros procesos ecosistémicos (Feng et al., 2013; Allen et al., 2017; Pennington et al., 2018; Calvo-Rodriguez et al., 2020). Si bien de forma natural existe una variabilidad inter e interanual en los patrones generales de lluvias de los BTS, se ha proyectado que los regímenes de lluvias se volverán aún más extremos aumentando la frecuencia e intensidad de eventos como El Niño y La Niña. En general los modelos climáticos predicen una disminución en la precipitación y un aumento del período seco para finales del siglo XXI (Chadwick et al., 2016; Allen et al., 2017; IPCC, 2021). Sin embargo, aún se sabe poco sobre cómo las alteraciones predichas por los modelos climáticos afectarán las dinámicas ecológicas de los BTS.

Para predecir las respuestas al cambio climático con mayor precisión, los modelos deben contemplar las relaciones entre los ciclos biogeoquímicos y sus principales impulsores ambientales: variación en el clima, propiedades físicas y químicas del suelo y composición de la comunidad vegetal (Waring et al., 2021). Los desafíos para predecir cambios en los patrones y procesos biogeoquímicos en los BTS radican en que estos son ecosistemas climáticamente variables, geológicamente complejos y biológicamente diversos (Townsend et al., 2008; Waring et al., 2021). En general, una de las mayores fuentes de incertidumbre en las proyecciones del cambio climático es la retroalimentación entre la biogeoquímica y el cambio climático (IPCC, 2021). Por ello, el aumento de Nr a escala global resulta alarmante. Estas nuevas entradas de N a los ecosistemas podrían tener efectos en su ciclo interno y en el balance estequiométrico con otros nutrientes (Steffen et al., 2015; Craine et al., 2018), aumentando la incertidumbre de la trayectoria del N a escala global (Elser, 2011; Craine et al., 2018).

Las evidencias indican que si bien los bosques tropicales siguen contribuyendo de manera significativa al balance de C terrestre, el calentamiento global producto de las presiones antropogénicas ha generado que el potencial de estos bosques para secuestrar C se esté viendo comprometido, y los bosques tropicales se están convirtiendo en fuentes netas de C emitido a la atmósfera en lugar de ser sumideros (Baccini et al., 2017; Siyum, 2020). Lo mismo se ha reportado para BTS que para años de El Niño secos y calurosos tienden a convertirse en una fuente neta de CO_2 (Castro et al., 2018). De igual manera, en la región tropical y subtropical, las grandes variaciones en la tasa de incremento del N_2O atmosférico, están correlacionadas con el fenómeno de El Niño y las anomalías en los flujos terrestres y oceánicos (Ji et al., 2019; Thompson et al., 2019). Y en el BTS se han reportado mayores emisiones de N_2O asociados a eventos de rehumedecimiento del suelo durante los años de El Niño (Calvo-Rodriguez et al., 2020). Si bien ya se cuenta con algunas evidencias del impacto de los cambios globales en estas regiones tropicales, aún es necesario hacer investigaciones que contribuyan a mejorar nuestra comprensión. En particular, esto es conveniente para entender el impacto sinérgico de los cambios en el régimen de precipitación y el aumento del depósito de N antropogénico, ya que muy pocos estudios contemplan ambos factores simultáneamente.

Esta investigación busca contribuir al conocimiento de la ecología de los BTS a diferentes escalas:

1) Escala global, a partir de información de mapas digitales, los cuales compilan datos de perfiles de suelo y sus capas ambientales, examinamos la variación espacial en las propiedades físicas, hidrológicas y químicas de lo suelo en las ecorregiones de BTS. Más allá de la descripción de las características físicas y biogeoquímicas del suelo, se analizó su relación con el clima. Hasta donde es nuestro conocimiento este esfuerzo de síntesis constituye el primero a escala pantropical.

2) Escala local, a partir de datos de campo se exploró el efecto del régimen de lluvias en el ciclo del N, además el efecto del incremento en la disponibilidad de N en su ciclo y su interacción con el régimen de lluvias. Para ello, se exploraron estos efectos en los suelos y la vegetación de dos bosques de la Península de Yucatán. La adición de N a diferencia de otros experimentos considera las tasas de depósito de N atmosférico esperadas en la región tropical para el año 2030, lo cual nos puede aportar datos más realistas de lo que podría ocurrir en estos ecosistemas bajo las condiciones actuales.

Los objetivos específicos fueron (1) determinar la variabilidad de las características del suelo entre las ecorregiones donde se distribuyen los BTS y (2) evaluar los posibles controles climáticos a largo plazo en los suelos de los BTS. Los cuales fueron abordados en el primer capítulo. Mientras que el objetivo del segundo capítulo fue (3) determinar los efectos de la precipitación media anual sobre el ciclo del N en los BTS de Yucatán. Y finalmente en el tercer capítulo, el objetivo fue (4) evaluar el impacto del aumento de las tasas de deposición de N en la dinámica del ciclo del N de dos BTS de Yucatán aunado al efecto de la variación en el régimen de precipitación.

Capítulo I

Artículo en preparación (Sustainability)

A Pan-tropical Overview of Soils across Tropic Dry Forest Ecoregions

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Resumen

Este estudio proporciona una descripción pantropical de los suelos en los paisajes del Bosque Tropical Seco (TDF), incluidas las características físicas y biogeoquímicas del suelo. Para cuantificar la distribución global de los suelos y su relación con el clima en las ecorregiones TDF, producimos una síntesis utilizando datos de 7500 puntos con campos cuadriculados de características litológicas, edáficas y climáticas. Nuestros análisis revelan que las ecorregiones TDF cubren rocas sedimentarias (57 %), metamórficas (22 %), volcánicas. (13 %) y plutónicas (7 %). La alta variabilidad (32 subórdenes) en los suelos ocurre en las ecorregiones TDF y domina las de baja fertilidad. Las propiedades del suelo mostraron una marcada heterogeneidad entre las regiones biogeográficas, con la profundidad del suelo variando en un orden de magnitud y las reservas orgánicas totales de C, N y P triplicadas. Los tamaños de las reservas de C y N orgánicos se correlacionaron negativamente con MAT y positivamente con MAP. Por el contrario, la distribución de las reservas de P del suelo fue influenciada positivamente tanto por MAT como por MAP, y probablemente también fue impulsada por la geoquímica del suelo, debido a la gran variación en el material original del suelo entre las regiones biogeográficas. Estas observaciones plantean cuestiones importantes, ya que el régimen climático y los tipos de materiales parentales conducen a la variabilidad biogeoquímica del suelo, así como al papel que desempeña la disponibilidad de agua en el suelo en el ciclo de nutrientes en estos suelos tropicales.

Abstract

This study provides a pantropical overview of soils in Tropical Dry Forest (TDF) landscapes, including soil physical and biogeochemical characteristics. To quantify the global distribution of soils and its relationship with climate in TDF ecoregions, we produced a synthesis using 7,500 points data with gridded fields of lithologic, edaphic and climatic characteristics. Our analyses reveal that TDF ecoregions covers sediments (57%), metamorphics (22%), volcanics (13%), and plutonics (7%) rocks. High variability [32 suborders] in soils occur in TDF ecoregions and dominate those of low fertility. Soil properties exhibited marked heterogeneity across biogeographic regions, with soil depth varying by an order of magnitude and total organic C, N, and P pools by threefold. Organic C and N pool sizes were negatively correlated with the MAT and positively correlated with MAP. By contrast, the distribution of soil P pools was positively influenced by both MAT and MAP, and probably was also driven by soil geochemistry, due to large variation in soil parent material across biogeographic regions. These observations raise important questions as the climate regime, and parent material types, drivers lead to the soil biogeochemical variability as well as the role that soil water availability plays in the cycling of nutrients in these tropical soils.

Keywords: carbon; nitrogen; phosphorus; soil climate relationships; soil fertility

1. Introduction

Tropical forest biome, including tropical dry forest (TDF), exhibit an exceptionally high soil biogeochemical heterogeneity from local to regional scales in response to the broad combination of abiotic (edaphic properties, climatic conditions) and abiotic (vegetation) conditions [1, 2]. So far, the reviews that includes an overview of the TDFs soils often inferred that those with medium- to high-fertility status dominate the landscapes [3, 4]. The conception that TDFs develop in regions with a high fertile soil probably was founded when these soils are compared to those in the humid counterpart or even to the savanna ecosystems [5,6]. Despite this frequent oversimplification, the literature about soils in TDF has documented their extreme spatial heterogeneity, reflecting a wide variety of climate, parent material, topography and vegetation [7]. Tropical landscapes commonly contain a large diversity of soils that range in age from the youngest (Entisols and Inceptisols) to the oldest (Ultisols] [8, 9, 10]; a factor that has influence in ecosystem function [11]. The complexity of the interactions among these environmental abiotic and biotic factors results in extreme heterogeneity in soil properties and soil-ecological processes, and consequently soils in TDFs is a highly dynamic biogeochemical system [12, 13, 14, 15]. Despite this ample evidence for the diversity of soils in the dry tropics, the popular concept of a tropical dry forest soil often suggests that are special groups of soils with specific properties and problems. For example, TDF ecosystems are under severe anthropogenic pressure [16, 17] and many evidence have highlighted that after native vegetation is cleared, soils were extremely fragile [18, 19] and incapable of sustaining the agroecosystem management [20, 21].

So, for future restoration efforts, as well as for conservation policy and management of the TDFs is imminent have a more complete soil base line to improve these practices and predict changes in the main nutrient's budgets that control native ecosystem responses to global environmental changes. For example, recent findings indicates that tropical forest is subject to huge loses of carbon (C) mainly in Africa and Neotropic regions, so are becoming a source of C emissions to the atmosphere [22, 23]. Ecological restoration not only recovers the landscape biodiversity, also promote C sequestration and nutrient conservation in terrestrial ecosystems and then have the potential to help offset many global changes in the global C cycle and other cycles as is the case of nitrogen (N) and phosphorus (P) [24, 25]. In this way, as the availability of N and P in soils controls the plant growth and C accumulation in TDF soils [26, 27], landscape-level variation in soil fertility is endpoint for restoration strategies in TDF landscapes, and its better understanding prevents achieving the restoration goals. On the other hand, future climate change [28] making some reference conditions potentially relevant to guide restoration efforts based on robust determinations of soil-climate relationships in tropical landscapes. Yet in many tropical ecosystems, we do not know the soil fertility variation in TDF across ecoregions, nor the climate drive feedbacks. Research is need to understand fundamental aspects of TDF' soils and the soil properties-climate relationships to improve methods for incorporating both soil diversity and climate variability into the practice of restoration ecology.

Since soils has been left out of the TDFs agenda, here we examined the spatial variation in soil physical, hydrological and chemical properties in TDF ecoregions noted for their marked taxonomic diversity across biogeographic regions. Our analysis was structured to target two specific research items by review the global data information available of multiple data repositories. First, we constructed a database of 7,500 points with gridded fields of lithologic, edaphic and climatic characteristics in 75 TDF ecoregions that has been previously described as TDF in a pantropical distribution. Second, due to sensitivity of TDFs to climate variations [23,29, 30] and assess the potential long-term climate controls on TDF soils, we analyzed the relationship of soil pH, cation exchange capacity (CEC), C and nutrient stocks with the mean annual temperature (MAT), mean annual precipitation (MAP) and aridity index at pantropical scale. Our analysis combines data across Afrotropic, Australasia, Indo-Malayan, Neotropic and Oceania biogeographical regions and cover a wide variety of climates, lithologies and soils, and were grouped according to the biogeographic distribution [31].

Our analysis show that soil properties exhibited marked heterogeneity across biogeographic regions, with total organic C and N pool sizes negatively correlated with the MAT and positively correlated with MAP. By contrast, the distribution of soil P pools was positively influenced by both MAT and MAP and reflect the large variation in soil parent material across biogeographic regions. Overall, the main results of this analysis reinforce the notion of the large soil diversity across tropical forest biome, and highly that TDFs soil are not as fertile as was thought. The last may be the reason way these regions have been largely transformed and abandoned, due the low aptitudes to substant agricultural land uses in the long-term, leading a broad mosaic of secondary tropical forests in different successional stages [32]. Also, our results indicate a significant relationship between the fertility of soils and climate characteristics that controls soil water availability in these landscapes.

2. Methods

2.1. Selection of Ecoregions

This study includes 75 ecoregions containing TDFs that previously were identified as this type of ecosystem by (*i*) Olson et al. [33], (*ii*) has been regionally described as TDF by local authors, or (*iii*) were included in the FAO [34] assessment of TDF (Table S1). Australia was excluded according to the World Wild Fund for Nature [WWF] delimitation of world ecoregions '*Tropical and subtropical dry broadleaf forest*' is only distributed in the New Caledonia Island and remains in isolated patches.

2.2. Selection of Sample Points

From each ecoregion, we created a 1 km^2 grid and then calculated the centroid of each cell as a sample point. We selected 100 sample points from all the centroids in a random block design to fully assess the range of climatic and edaphic variation within each ecoregion (Figure 1). We assumed similar conditions within each ecoregion because they are defined as geographical regions that are characterized by specific ecological patterns, including soil health, flora and fauna, climatic conditions, among other factors [33] . All spatial analysis were conducted in ArcGIS 10.2.1. Because the surface of each ecoregion differs greatly among them, we could not select different number of sample points for each ecoregion as this would result in an overrepresentation of values from larger ecoregions. Also, we assumed similar conditions within each ecoregion because they are defined as geographical regions that are characterized by specific ecological patterns, including soil, flora and fauna, climatic conditions, among other factors.

2.3. Climatic and Edaphic Metrics

For each sample point, climatic, lithological and edaphic data were obtained from different maps and data repositories: NASA Earth Observation (NEO, https://neo.sci.gsfc.nasa.gov/), Climatic Hazards Center- UC Santa (https://www.chc.ucsb.edu/about), Numerical Terradynamic Simulation Group (NTSG)- University of Montana (https://www.ntsg.umt.edu/), Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) (data at 5.6 km resolution), Composition of the Geological map of the world (https://ccgm.org/en/home/168-lithological-map-of-the-world-9782917310250.html) (data at 1 km resolution), and for the Biogeochemical Dynamics NASA (https://daac.ornl.gov/) and SoilGrids (https://soilgrids.org/; data at 1 km resolution). Soils are described at suborder level to USDA soil taxonomy and were grouped according to their fertility (in low, medium and high fertility) and water retention capacity (low, medium and high). Eight climatic metrics were examined, including indicatives of temperature as MAT, mean daily minimum temperature in coolest month and mean daily maximum temperature in warmest month (hearafter, minimum temperature and maximum temperature, respectively), and indicatives of site water availability variables encompassing MAP, precipitation in the driest month, precipitation in the wettest month, and total precipitation in the rainy season, and Lang aridity index (that is, the ratio between annual precipitation and temperature). Our approach integrates the climatic variability for a 11-year period (2004 to 2014) at Pantropical scale, and we calculated average climate variables for each site. We also computed several metrics of soils that account the physical and water retention properties encompassing the following: soil depth, bulk density, coarse fragments, clay content (representing soil texture), field capacity, water holding capacity and the wilting point, and compiled information on soil fertility properties such as pH, CEC, and the organic carbon (organic C), total nitrogen (total N), and total phosphorus (total P) stocks. Each metric was processed and harmonized to standard units.

2.4. Data Analysis

All statistical analyses were conducted in R version 4.0.3 [35]. To assess the climatic and edaphic characteristics across the 75 ecoregions, we grouped each ecoregion in five biogeographic regions according to the geographic distribution (Afrotropic, Australasia, Indo-Malayan, Neotropic, and Oceania). We conducted ANOVA to explore soil and climate variations across biogeographic regions.

The key axes of the multi-dimensional space of soil properties were identified using principal component analysis (PCA). Each variable was standardized. From the PCA results we extracted the explained variance of each component and the loadings of the soil properties, indicating the contribution of each variable to the component. A total of 7,497 sample points (three points had not climatic and/or edaphic data) were obtained of divers database, this data set allows to capture the large climatic and edaphic variation across world tropical dry forest region. We performed the PCA using the function PCA implemented in the R package. Finally, we analyzed the predictive importance of three climate variables (MAT, MAP, and Lang aridity index) on five soil fertility properties (pH, CEC, organic C, total N, and total P) using Pearson´s correlation analysis.

3. Results

The seventy-five ecoregions of this study are distributed in five biogeographic regions and four continents (Figure 1). The largest biogeographic region is the Afrotropic (14,600,868 km^2) accounted for 67.3% of the global surface of TDF ecoregions evaluated and including 23 ecoregions (Table S1). The second largest is the Neotropic that represents the 24.4% of worldwide surface evaluated and include the most abundant variety of ecoregions (34 ecoregions), followed by the Indo-Malayan biogeographic region (7.9% and 12 ecoregions), meanwhile Australasian and Oceanian biogeographic regions combined represents less than 0.5% and include a total of six ecoregions.

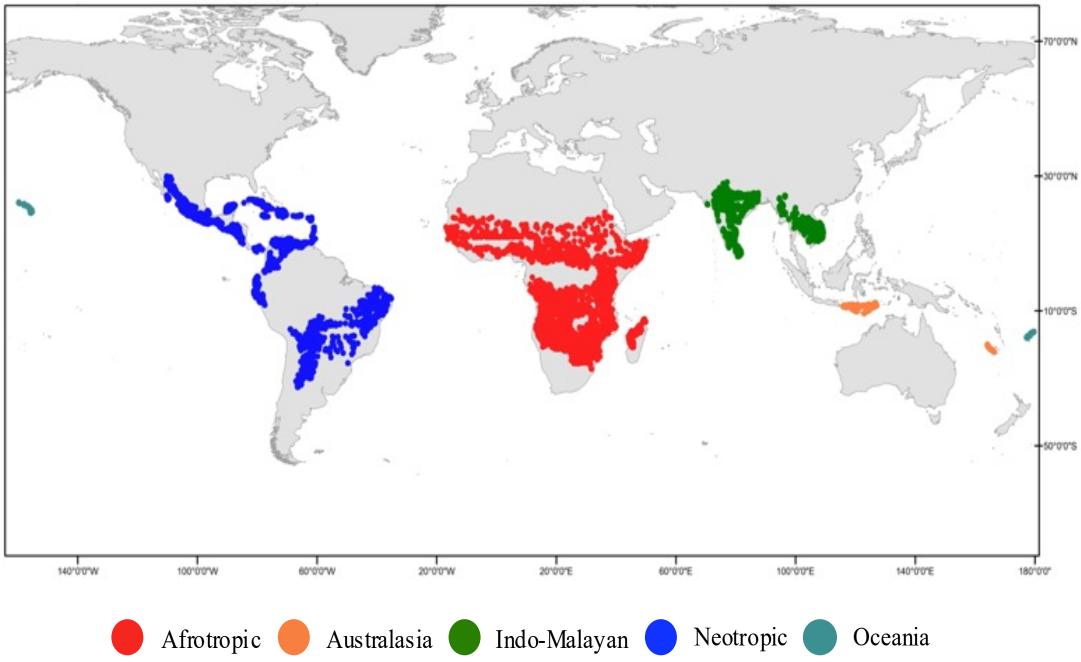

Figure 1. Tropical dry forest ecoregions. Each circle indicates the distribution of the 100 samples points within each ecoregion, and colors indicates the five studied biogeographic regions.

3.1. Global Lithological Classes and Soils

Tropical dry forest ecoregions are developed in at least twelve lithological classes. The sampling points includes lands that covers sediments (59%), metamorphic (22%), volcanic (11%), and plutonic (7%) rocks (Figure 2). Significant regional differences in lithology distribution are observable: e.g., Oceania is the biogeographic region with lowest lithological variety, meanwhile Neotropic is the only one that have all the lithological classes. On the other hand, sediments rock units dominate the Neotropic, Australasia, Afrotropic and Indo-Malayan landscapes (represent 76, 60, 49 and 47% of the total evaluated area in each biogeographic region, respectively; with abundant carbonate containing rock units in Australasia and Neotropic, 21 and 14% of the total area, respectively) while represent only 8% in ecoregions of Oceania (with a participation of carbonate containing rocks of 3.5% of the total area).

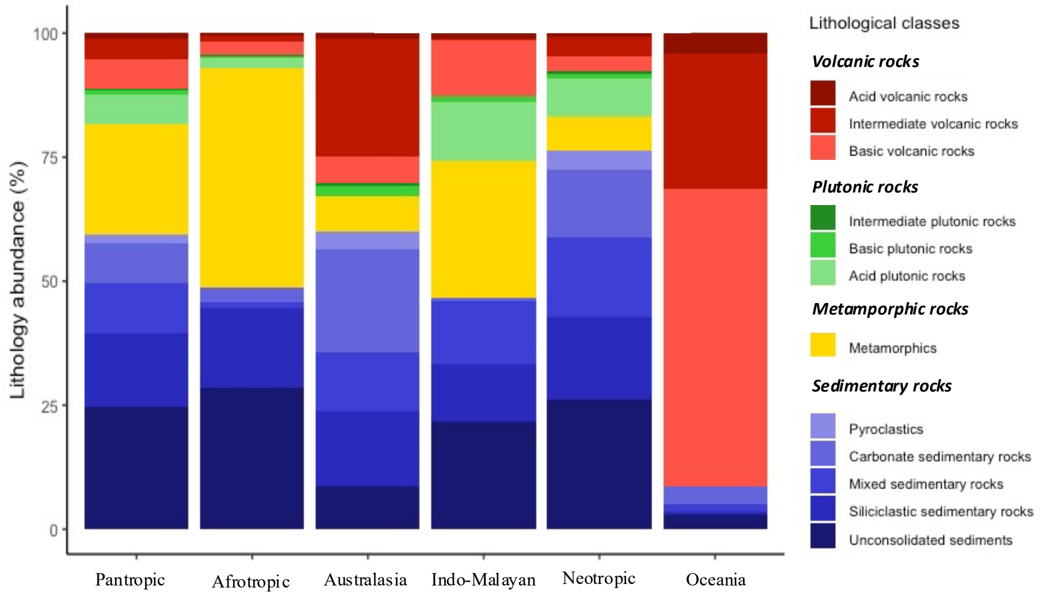

Figure 2. Lithology in tropical dry forest ecoregions within biogeographic regions and at pantropical scale.

Our rationale was to quantify the very wide variation of soil taxa found throughout tropical biogeographic regions of Africa, America and Asia, and our results are presented in Figure 3. A total of 32 soil suborders were identified. The 69 % of the soils corresponds to five suborders (Udults, Ustalfs, Ustolls, Usterts and Ustox). The Neotropic is the biogeographic region with the largest soil diversity, and account 28 of the 32 suborders identified (data not showed). In contrast, Australasia shows lowest variety of soils with only eight suborders. Moreover, Oceania has the double of soil suborders than Australasia in a smaller evaluated area (13,308 and 90,548 km^2, respectively; Table S1). Soils with low fertility and medium water retention capacity dominates TDF ecoregions at pantropical scale (Figure 3b).

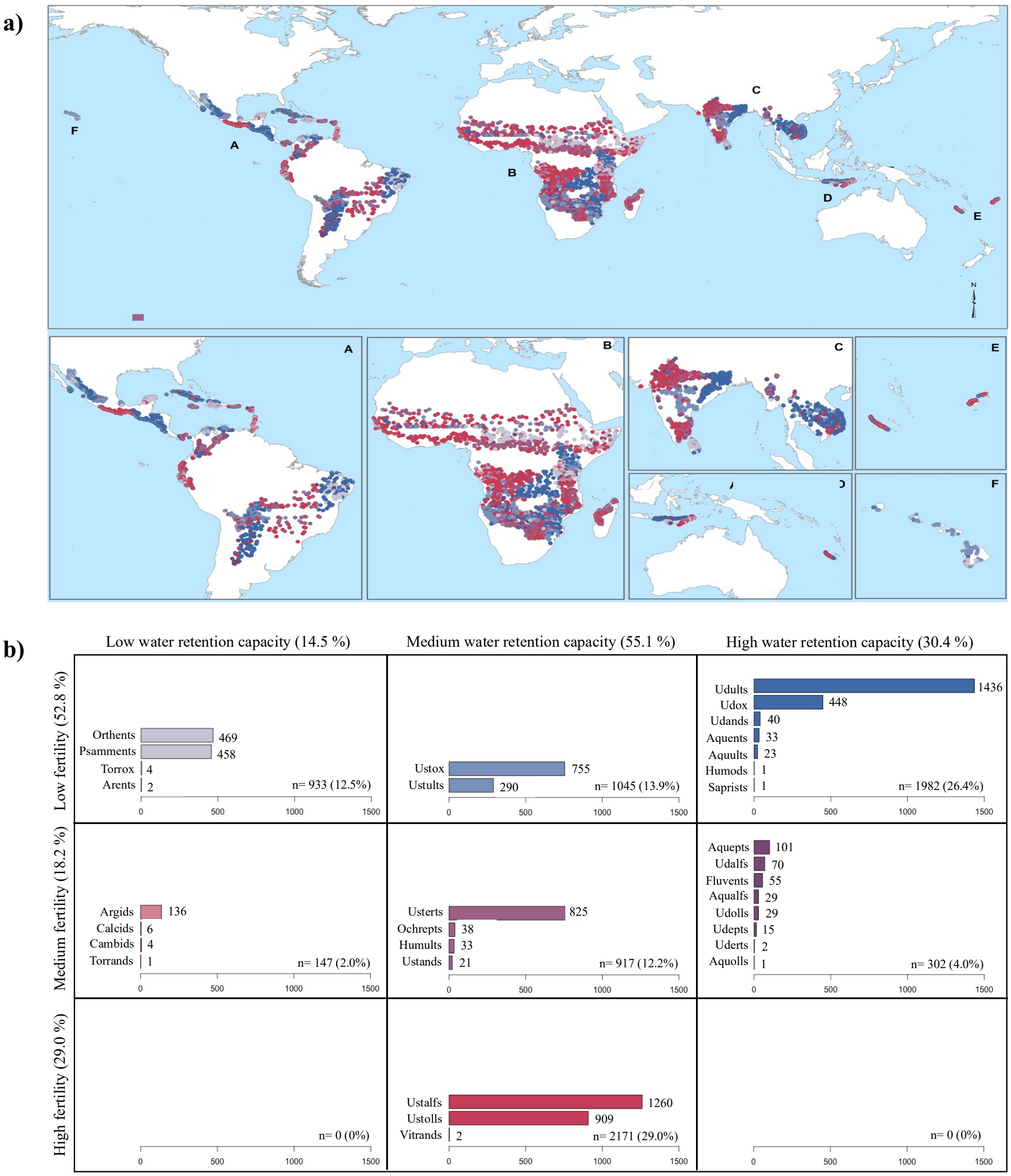

Figure 3. Soil distribution according to their fertility and water retention capacity in tropical dry forest ecoregions at the pantropical scale (**a**); filled color symbols indicates the combination of the soil fertility with the water retention capacity (as is indicated in panel b), and capital letters indicates the biogeographic region: A, Neotropic; B, Afrotropic; C, Indo-Malayan; D, Australasia; and E, Oceania. Global soil suborders in tropical dry forest ecoregions, the horizontal grids indicate the soil fertility (low, medium, and high) and the vertical ones the water retention capacity (low, medium, and high) (**b**).

There is a large variation in soil properties at pantropical scale (Table S2). The deepest soils are in the Afrotropic with a mean of 2.53 m, meanwhile the most superficial are in Oceania (mean = 0.30 m in depth; Figure 4a, Figure S1). Oceania' soils have the lowest bulk density, and soils with highest density are in Indo-Malayan biogeographic region (1.23 and 1.52 g cm^{-3}, respectively; Figure 4b, Figure S1). Coarse fragments are most abundant in Indo-Malayan' soils, meanwhile soils of Australasia show the lowest content of fragments (Figure 4c, Figure S1). The clay content is highest in soils of Indo-Malayan and Neotropic biogeographic regions (38.8 and 38.2 percent, respectively), and lowest in soils of Afrotropic (29.9 percent) (Figure 4d, Figure S1).

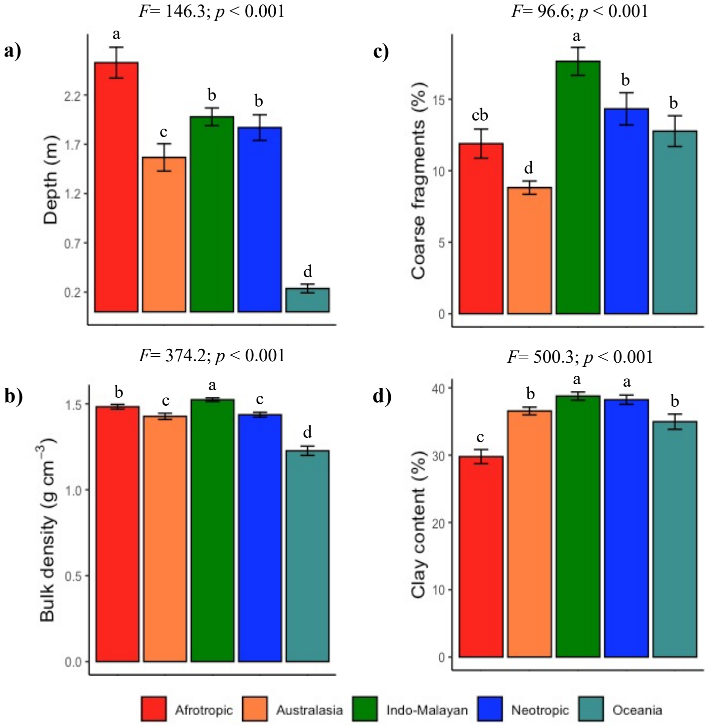

Figure 4. Spatial variation in soil physical properties. Panels indicates the soil depth (**a**), bulk density (**b**), and coarse fragment (**c**) and clay (**d**) contents. Values are mean ± 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic regions.

Significant variation in soil water retention is observed amongst biogeographic regions (Figure 5). For example, although the average of field capacity varies in a short range across biogeographic regions (from 399.7 mm in Afrotropic to 418.7 mm in Australasia) differences are significant (Figure 5a, Figure S2). In addition, soils of Afrotropic have the lowest wilting point and water holding capacity (Figure 5b,c, Figure S2). In contrast, soils of Indo-Malayan biogeographic region have the highest wilting point, meanwhile soils of Australasia have the highest water holding capacity.

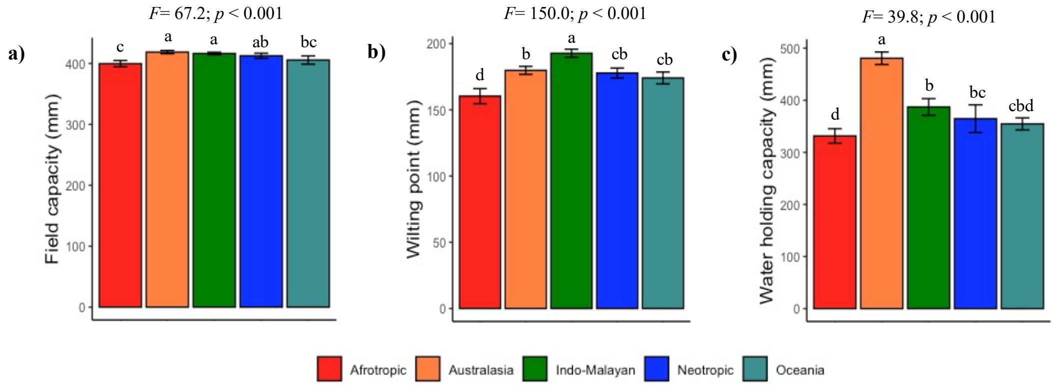

Figure 5. Spatial variation in soil water retention capacity. Panels indicates soil field capacity (**a**), wilting point (**b**) and water holding capacity (**c**). Values are mean ± 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic regions.

The average of soil pH across biogeographic regions varied from 5.7 to 6.6 and increase following the order Australasia < Oceania < Afrotropic < Neotropic < Indo-Malayan (Figure 6a, Figure S3). On other hand, soil CEC is lowest in Afrotropic followed by Australasia, and highest in soils of Indo-Malayan biogeographic region (Figure 6b, Figure S3). Soils of the Neotropic and Oceania constituted an intermediate, statistically homogeneous group ($p > 0.05$). Also, we found an increasing and significant gradient in soil organic C and total N stocks in the direction of Afrotropic ~ Indo-Malayan < Neotropic < Australasia < Oceania (Figure 6 c,d, Figure S3). Although the gradient of C and N stocks detected across biogeographic regions was not observed in the case of soil P stocks, Afrotropic (and also Australasia) have the P-poorest soils, while Oceania has the P-richest soils (Figure 6e, Figure S3).

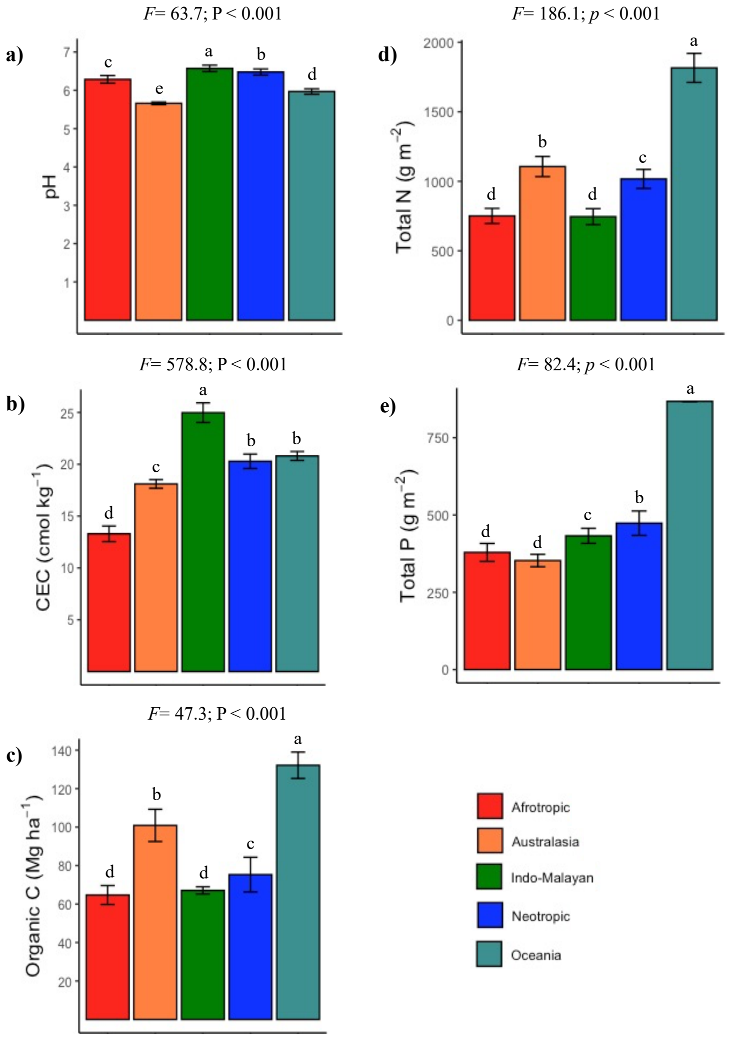

Figure 6. Spatial variation in soil fertility properties. Panels indicates soil pH (**a**) and cation exchange capacity (**b**), and organic carbon (**c**), total nitrogen (**d**) and total phosphorus (**e**) contents. Values are mean ± 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic regions.

The PCA conducted across the edaphic dataset allowed to identify in a simple way which soil features are the most distinguished at each biogeographic regions generating its clear separation between them. On the one hand, Afrotropic are characterized by having the deepest soils, meanwhile Oceania is the biogeographic region that have the most fertile soils with largest stocks of C, N and P (Figure 7). On the other hand, the Indo-Malayan separates of the other ones mainly in response to soil water retention metrics, and clay content. The first two principal components explain 77 percent of the data variation (Table 1). Across the entire data set, the first principal component summarized 42 percent of the variation in soil metrics, particularly the variables that loaded most strongly into the first PC axe were soil bulk density and depth ($r = 0.98$, $p < 0.01$ and $r = 0.93$, $p < 0.05$, respectively) and the organic C and the total N stocks ($r = -0.98$, $p < 0.01$; in both cases). The second principal component (PC2) accounts the 34 percent of variation, and the highest correlation to this axis was obtained by the wilting point, the clay content, and the CEC ($r = 0.96$, $p < 0.01$ in the cases of wilting point and clay content; and $r = 0.94$, $p = 0.05$, in the case of CEC).

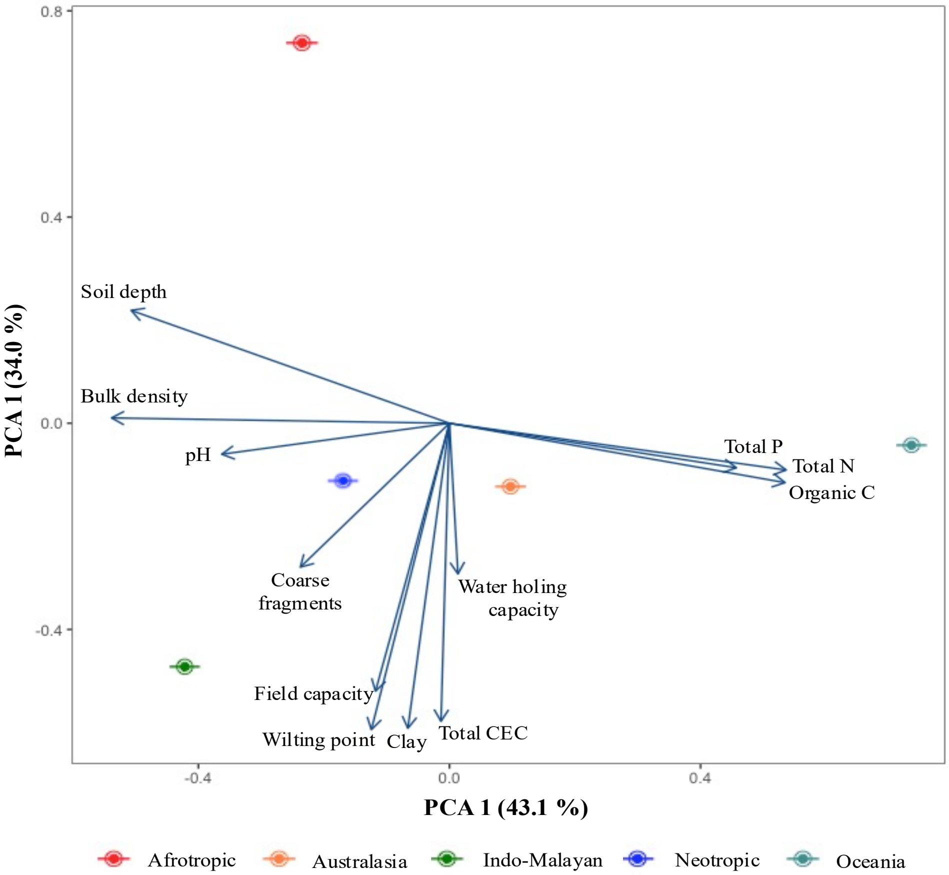

Figure 7. Principal component analysis (PCA) biplot of the edaphic metrics in tropical dry forest ecoregions at the pantropical scale.

Table 1. Eigenvalues, cumulative percent variation, and eigenvectors of the first three principal components (*PCs*) for the soil metrics in tropical dry forest ecoregions at the pantropical scale.

		PC1	**PC2**	**PC3**
Eigenvalue		5.168	4.307	2.169
Cumulative variation percent		43.06	76.99	98.69
Eigenvectors				
	Soil depth	-0.925	0.355	0.128
	Bulk density	-0.982	0.017	0.162
	Coarse fragments	-0.434	-0.452	-0.772
	Clay content	-0.121	-0.958	0.019
	Field capacity	-0.215	-0.842	0.487
	Water holding capacity	0.025	-0.473	0.877
	Wilting point	-0.227	-0.963	0.011
	pH	-0.662	-0.097	-0.732
	Cation exchange capacity	-0.025	-0.936	-0.334
	Organic carbon	0.976	-0.187	-0.101
	Total nitrogen	0.979	-0.147	-0.119
	Total phosphorus	0.834	-0.140	-0.533

3.3. Climate and Soil Fertility Relationships

The MAT across the ecoregions is in the range between 22.0 to 37.7 ºC with a pantropical mean of 29.2 ºC (Table S2). The MAP is 1143.7 mm (range from 320.5 to 2294.1 mm) and in average TDF ecoregions suffer 7.4 dry months (precipitation is less than 100 mm) and 4.4 months of hydric stress for vegetation. The hottest ecoregions are in Afrotropic and Indo-Malayan biogeographic regions, both with MAT of 30.4 ºC, while Australasia and Oceania support lowest MATs (Figure 8a). Also, the Afrotropic is the driest biogeographic region (MAP of 913 mm), meanwhile the wettest biogeographic regions are Australasia and Oceania (MAP of 1589 and 1516 mm, respectively) (Figure 8b). We found an increasing and significant gradient of aridity in the direction of Australasia ~ Oceania < Indo-Malayan < Neotropic < Afrotropic (Figure 8c).

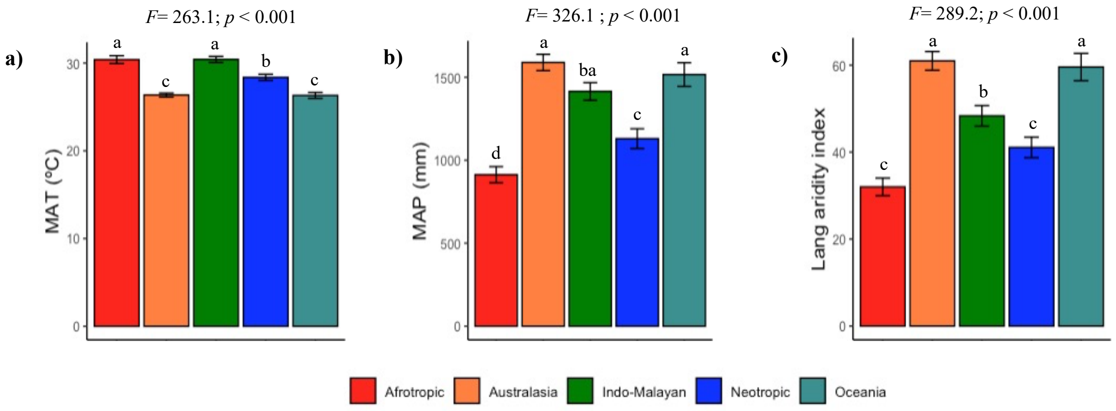

Figure 8. Spatial variation in mean annual temperature (**a**), mean annual precipitation (**b**) and Lang aridity index (**c**). Values are mean ± 1SE and different letters indicate significant difference ($p < 0.05$) across biogeographic regions.

Overall, pH was the soil property most strongly related to climate (values increase with MAT, while decrease with MAP and aridity index) (Figure 9 a-c; Table S3). In contrast, CEC was the least climate-related soil characteristic, with no statistically significant relationship with MAP (Figure 9 d-f); but CEC was more related with the precipitation in both the driest and the wettest months (Table S3). Soil C and total N stocks decreased with increase in MAT while increased with precipitation amount (Figure 9 g-l). The strongest effect of precipitation regimen was observed on soil C stock and was in response to increase in rainfall amount during the driest month (Table S3). Phosphorus stocks in soils were, also, most strongly related to precipitation in the driest month, followed by minimum temperature (Figure 9 m-o; Table S3); the size of pools of this rock-derived nutrient decreased with increase in drought (i.e. a decrease in MAP and in aridity index; Figure 9).

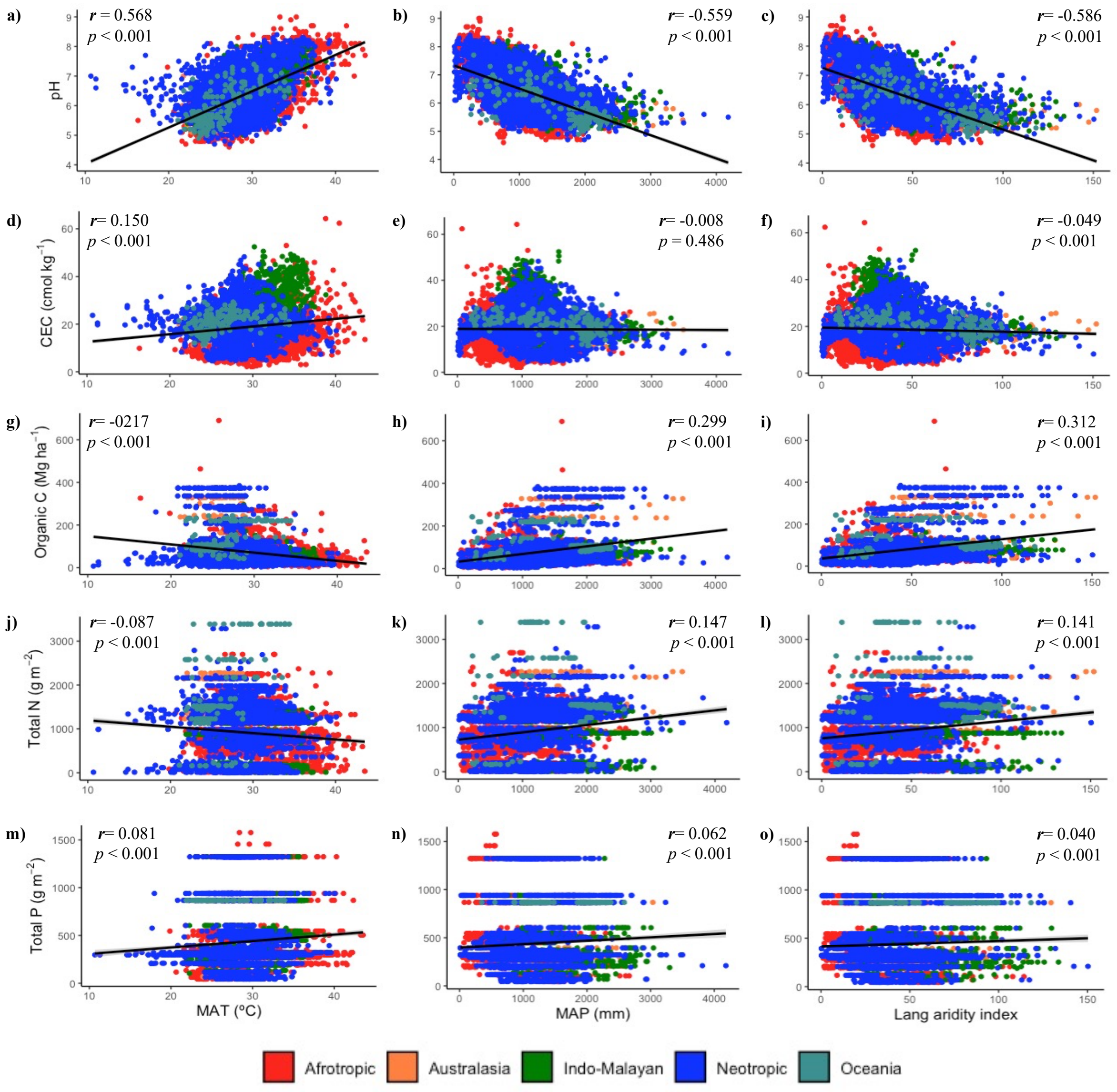

Figure 9. Relationships between soil pH, cation exchange capacity, and organic carbon, total nitrogen and total phosphorus contents and main climate drivers of the tropical dry forest distribution and function. Colored points show data for each biogeographic region. Black lines show pantropical bivariate relationships.

4. Discussion

As far as we are aware, our analysis is the first effort of synthesize and characterized the large soil diversity of the TDF ecoregions at pantropical scale. Recently Waring et al. [7] provides an overview of soil biogeochemistry across the Americas TDFs, allowing to have a better understanding of the Neotropic region, however there is no similar one at global scale. It doesn't have ecological sense a single generalization that encompasses all the TDF’ soils, as “typical” TDFs soils, nevertheless, for managing and conservation purposes could be useful reduce the great heterogeneity of this component of the ecosystem into a few groups. In this attempt we grouped the ecoregions in to five biogeographic regions, according to the World Wildlife Fund´s global priority ecoregions assessment [33]. This approach led us to identify the major differences among biogeographic regions, that reflects the large parent material diversity and climate variability that determine the soil characteristics in tropical forest biome [1, 7, 36].

4.1. Soil Diversity in the Tropical Dry Forest Biome

Our study showed that at pantropical resolution TDF ecoregions capture enormous variability in the composition of soil parent material, accounting twelve of the different sixteen global lithological classes [37], reinforcing the idea that tropical forest biogeochemistry is often highly heterogeneous at local and regional scales [1, 38]. Despite this large variability in rock types, with largest diversity of lithologies in the Neotropic, generally TDF landscapes are developed on sediments with abundant carbonate containing rock units. This lithological variation influences spatial variability in soil properties and terrestrial ecosystem biogeochemistry [4, 39], by determining the supply of rock-derived nutrients that are essential for plant growth and microbial activity [40], and limit ecosystem function in tropical forest biome as is the case of P [41].

Our data also shows that soil taxa in TDF ecoregions are diverse at a pantropical scale. Common soils include nutrient-poor soils that are either well drained that have clay-enriched subsoils (Uldults) or that are iron and aluminium-rich, and friable (Udox); and soils with medium (Ustox and Ustults) or low capacity for water retention as sandy soils (Orthents) including those deposited by rivers on plains (Psamments). Also, TDF ecoregions include deep, organic-rich soils that are often highly fertile (Ustalfs and Ustolls, respectively), and rocky and shallow soils on slopes (Usterts). Our study captured the large soil heterogeneity and the principal component analysis allows to remark the importance of some soil physical properties, like depth and the clay content that influence the water retention capacity across the soil profile and therefore control the ecosystem biogeochemistry [15,42, 43]. Although soil properties exhibited marked heterogeneity across biogeographic regions, with mean soil depth varying by an order of magnitude and total organic C, N, and P pools by threefold, our data indicate that TDF ecoregions are dominated by nutrient-poor soils with a medium capacity for retain the rainfall water.

4.2. Are Tropical Dry Forest Soils Fertile?

Our approach of classify the soils suborders into three major fertility groups allowed us a better understanding of the main soil characteristics, breaking downs the generalized idea that soils in TDF landscapes are fertile [6, 44]. Moreover, our data indicates that only 29% of the soil data across ecoregions support this idea, contrastingly ~53% of soil evaluated were cataloged as nutrient-poor. This finding of our study subscribes to the recent proposal that more than half of the dry forests occur in highly weathered, leached, and nutrient-impoverished soils [43, 45]. The large proportion of infertile soils in the TDFs seems to be like to those of the humid counterpart in the tropical forest biome, where soils are classified as mildly to severely infertile soils since have low nutrient supplies, particularly P for plant and microbial demands [46, 47]. On the other hand, the often suggestion in the literature that TDFs are developed on fertile soils seems to be influenced by the soil properties of Neotropic, a biogeographic region where TDF ecosystems have been extensively studied [see efforts of synthesis in 3, 44,48, 49, 50,51].

4.3. Vulnerability of Tropical Dry Forest Soils to Disturbances

We analyze the relative importance of twelve soil properties on the predictability of soils at biogeographic region scale using a PCA. By analyzing these set of soil properties across major TDF ecoregions and biogeographic regions in the multivariate PCA, we showed that the first and most important axis represents soil chemical and soil physical properties and is driven by C and nutrient stocks, and soil density and depth, and clearly separated the shallow and nutrient-rich soils of Oceania. The second axis, related to water-retention capacity, was driven by clay content and related to soil weathering indicated by the CEC and separated the high weathered soils of Africa with lowest capacity of water-retention, from those of Indo-

Malayan with high-CEC and a good water-retention; and shows a gradient related to soil fertility. Thus, we find that differentiation between soils of Afrotropic and Oceania is largely explained by depth and nutrient stocks.

Oceania is the biogeographic region that accounts the largest C, N and P stocks, a crude measure of soil fertility status [52]. The fertility observed in Oceania' soils is related to the large percent of volcanic parent material (90% of the area is covered by of volcanic rocks) that in combination to low precipitation, leads to moderate to high fertility soils. According to the conceptual model of the development of soils [53], is expected the large total P stock in soils that are at least 50% greater than in other biogeographic regions, and is expected also large Ca, K and Mg pools since base cations as P are rock-derived elements [54, 55]. In the Hawaiian region the volcanic activities leading to young and less weathered soils, as has been demonstrated across the natural precipitation gradient across the Hawai´i island where the soil nutrient concentrations as N, and base cations decreases with the increase in the annual precipitation amount [46]. Although much of the available cations like the calcium and magnesium weathered from primary minerals get lost rapidly, P is retained within the system in Hawaiian' soils [54], and in young volcanic TDF' soils in Mexico [56, 57].

In contrast, the Afrotropic' TDF ecoregions develops under the least fertility conditions in combination to the greatest pantropical aridity (i.e. the hottest temperatures and the lowest rainfall amounts). These low fertility soils could be the reason why the African TDFs occupy the low end of global tropical forest biomass range [58]. The deep and poor African soils may reflect a longer pedogenetic process in contrast to the those in other biogeographic regions; for example, soils of Africa, particularly those in west of the continent are very weathered [59, 60], as reflect the low CEC observed in our study. Moreover, other nutrient-poor soils in Africa may be reflect the low availability of soil water. In general, this biogeographic region presents the lowest values of clay content, a soil characteristic that drive soil water content [61], a factor that modulate the phenological patterns and biogeochemistry in TDF ecosystems [62, 63].

Deepest and nutrient-poor Afrotropic soils and nutrient-rich but shallow Oceania soils constitutes two special and extreme situations for both the soil conservation politics and the practice of restoration in TDF landscapes. On the one hand, the shallow and rock soils of Oceania are specially sensitives to land-use and land-cover change practices despite their large nutrient stocks. Thus, the conservation of these soils is a priority considering that this region shows the largest proportion of land in a degraded state (more than of 35%) [64]. On the other hand, besides of the lowest water retention capacity of their soils Afrotropic biogeographic region suffer the strongest aridity across studied regions. Also, Africa suffer the largest deforestation across continents, including continuous increase in the rate of deforestation in the last 30 years (1990-2020) [64]. Thus, soil resources could be the most important limitations for the success of TDF restoration plans. In any case the importance of vegetation root system and water-use strategies is absolutely priority for the selection of species to include in the restoration plans of TDFs, mainly in Afrotropic.

4.4. Vulnerability of Soil C, N and P to Ongoing Climate Change: Some Clues Derived from the Relationship between Soil Fertility and Climate in TDF Ecoregions

Our data set allow to have a better pantropical overview of how climatic variations influence the soil fertility of this ecosystem. The aridity expressed as the Lang aridity index positively correlates with organic C and nutrient stocks (Figure 9), reflecting the effects of precipitation amount in the driest month rather than precipitation in the wettest month or along the rainy season (Table S3). This C pattern in soils across TDF landscapes is consistent with the observed sensitivity of ecosystem function to precipitation amount in the dry season [15, 65, 66, 67].

Our analysis also suggest that warming could increases soil C and N stocks (Figure 9). The sensitivity of soil C stocks to temperature was mainly related to variations in maximum temperature and weaker related with the increase in minimum temperature (Table S3). The strong relationships observed in soil C stocks in TDF ecoregions with temperature and precipitation regime suggest a complex sensitivity of soil biogeochemistry to the global climate change. Moreover, in a recent study of TDF fires at pantropical scale Corona-Núñez and Campo [68] found that the most extensive fires and burned biomass during 1997-2020 period were driven by climate, particularly related with water stress (low precipitation, high temperature and an increase in aridity), with strongest effects in El Niño years. Given that global warming continues and further variability in precipitation regime including global monsoon precipitation and the severity of dry events are projected [28], the topic of the present study warrants subsequent investigation.

5. Conclusions

Soil data have accumulated that make it impossible to ignore the diversity of soils found in in the dry tropical forest ecoregions. Even small-scale demonstrated the diversity of soils of the dry tropics, with strong consequences for soil function [14, 69]. Such data document that misconceptions about tropical dry forest soils are fertile, still invoked frequently, oversimplifies the complexity and diversity of soils in the dry forest tropical ecoregions and should be examined. We also conclude that detailed understanding of soil diversity at all spatial scales and their relationship with the climate may be required to accurately predict the impact of global warming on forest carbon and improve restoration of tropical dry forest ecosystems under future scenarios.

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AUTHOR CONTRIBUTIONS

Conceptualization, M.P-D., J.C. and C.P.G.; investigation, M.P-D. G.R.T. C.P.G. and J.C.; data analysis, A.R-V., M.P-D. and G.R.T.; original draft preparation, A.R-V. and J.C.; writing – review & editing, J.C. with input from all authors; funding acquisition, C.P.G.

DATA AVAILABILITY STATEMENT

Data supporting the reported results, datasets generated during the study, can be found in the supplementary information included with this manuscript.

CONFLICTS OF INTEREST

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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Supplementary material

Table S1. Biogeographic regions and ecoregions included in this study, their surfaces and centroids. Number of ecoregions within each biogeographic region in parentheses.

Biogeographic region/*Ecoregion*	**Surface (km^2)**	**Centroided *X***	**Centroided *Y***
Afrotropic (23)			
Angolan Miombo Woodlands	690,767	18.1260	-12.4747
Angolan Mopane Woodlands	146,990	15.4562	-17.9383
Central Zambezian Miombo Woodlands	1,216,745	28.6362	-9.5779
East Sudanian Savanna	935,406	25.0921	8.4321
Eastern Miombo Woodlands	505,945	37.2378	-12.2385
Guinean Forest-Savanna Mosaic	687,746	-1.4409	8.8744
Itigi-Sumbu Thicket	7,937	32.1708	-7.1458
Kalahari Acacia-Baikiaea Woodlands	384,289	22.9014	-21.0716
Madagascar Dry Deciduous Forests	165,736	46.3538	-16.9212
Mandara Plateau Mosaic	7,735	13.7002	10.5155
Northern Acacia-Commiphora Bushlands and Thickets	325,257	36.8838	0.6593
Northern Congolian Forest-Savanna Mosaic	711,853	22.0592	5.4963
Sahelian Acacia Savanna	3,258,413	14.8427	14.8427
Somali Acacia-Commiphora Bushlands and Thickets	1,063,581	43.4991	5.8965
Southern Acacia-Commiphora Bushlands and Thickets	228,394	35.3313	-4.4023
Southern Africa Bushveld	261,206	28.5114	-22.6068
Southern Congolian Forest-Savanna Mosaic	573,357	21.9466	-5.7231
Southern Miombo Woodlands	448,286	31.3375	-17.5322
West Sudanian Savanna	1,705,016	-0.9302	11.8560
Western Congolian Forest-Savanna Mosaic	416,006	15.0456	-5.3282
Zambezian And Mopane Woodlands	530,736	31.0127	31.0127
Zambezian Baikiaea Woodlands	289,048	21.2278	-17.2735
Zambezian Cryptosepalum Dry Forests	40,419	23.6269	-13.9103
Total	14,600,868		

Australasia (4)			
Lesser Sundas Deciduous Forests	40,171	119.6750	-8.5723
New Caledonia Dry Forests	5,078	165.2656	-21.3263
Sumba Deciduous Forests	11,037	119.9495	-9.7607
Timor and Wetar Deciduous Forest	34,262	125.0775	-9.2090
Total	90,548		
Indo-Malayan (12)			
Central Deccan Plateau Dry Deciduous Forests	267,321	78.4078	18.8029
Central Indochina Dry Forests	343,625	103.3078	15.4735
Chhota-Nagpur Dry Deciduous Forests	145,384	85.4464	23.6245
East Deccan Dry-Evergreen Forests	26,570	79.6699	11.9025
Irrawaddy Dry Forests	39,996	95.5034	20.7242
Khathiar-Gir Dry Deciduous Forests	321,576	75.2392	24.4865
Narmada Valley Dry Deciduous Forests	199,313	77.9374	22.7605
Northern Dry Deciduous Forests	66,246	83.2940	20.4873
South Deccan Plateau Dry Deciduous Forests	85,460	77.6871	11.6999
Southeastern Indochina Dry Evergreen Forests	130,631	106.1723	13.2054
Southern Vietnam Lowland Dry Forests	36,953	108.5678	13.5358
Sri Lanka Dry-Zone Dry Evergreen Forests	49,122	80.8066	7.7860
Total	1,712,197		
Neotropic (34)			
Apure-Villavicencio Dry Forests	69,342	-70.9928	7.0125
Atlantic Dry Forests	120,431	-43.2759	-12.4547
Bajio Dry Forests	42,558	-102.0617	20.4620
Balsas Dry Forests	69,149	-100.1565	18.4628
Bolivian Montane Dry Forests	81,285	-65.3952	-18.8621
Caatinga	750,198	-39.8611	-8.6512
Cauca Valley Dry Forests	7,367	-76.0523	4.7661
Central American Dry Forests	71,562	-87.4874	13.2731
Cerrado	2,060,259	78.4078	18.8029
Chiapas Depression Dry Forests	15,155	-92.7963	16.2560
Chiquitano Dry Forests	249,035	-60.5090	-16.1166
Cuban Dry Forests	76,074	-78.8727	21.6632
Dry Chaco	965,297	-62.7380	-25.1395
Ecuadorian Dry Forests	21,204	-80.2332	-1.3603
Hispaniolan Dry Forests	17,244	-71.7766	18.8807

Jalisco Dry Forests	29,331	-104.2313	19.5750
Jamaican Dry Forests	2,553	-77.4184	18.0427
La Costa Xeric Shrublands	70,180	-66.1586	9.7250
Lara-Falcon Dry Forests	17,494	-69.1874	10.9102
Lesser Antillean Dry Forests	960	-61.3909	13.3826
Magdalena Valley Dry Forests	165,736	46.3538	-16.9212
Maracaibo Dry Forests	31,031	-71.4197	-71.4197
Maranon Dry Forests	11,465	-78.2976	-78.2976
Panamanian Dry Forests	5,192	-80.2900	8.1613
Patia Valley Dry Forests	2,263	-77.1909	1.8907
Puerto Rican Dry Forests	1,405	-66.5322	18.0330
Sierra De La Laguna Dry Forests	4,726	-109.9019	23.5623
Sinai Valley Dry Forests	93,173	-74.0584	10.0899
Sinaloan Dry Forests	25,666	-106.5990	24.3006
Sonoran-Sinaloan Transition Subtropical Dry Forests	62,547	-109.5851	27.9847
Southern Pacific Dry Forests	46,037	-97.4684	-97.4684
Tumbes-Piura Dry Forests	41,450	-80.1856	-5.1743
Veracruz Dry Forests	7,400	-96.4209	19.0561
Yucatan Dry Forests	56,488	-89.2165	20.4516
Total	5,291,257		
Oceania (2)			
Hawaiian High Islands: *Hawaii Tropical Dry Forests*	5,751	-156.2946	20.1273
Fiji Tropical Dry Forests	7,557	170.1973	-17.3244
Total	13,308		
Pantropical total	21,708,178		

Table S2. Statistic metrics of climate and soil variables selected for this study.

	Mean	**CV (%)**	**Qu. (0.25)**	**Median**	**Qu. (0.75)**	**Range**
Climate						
Mean annual temperature (ºC)	29.2	12.5	26.6	28.9	31.5	10.7- 43.5
Minimum temperature of the coldest month (ºC)	24.4	11.5	22.9	24.4	25.9	7.7- 41.2
Maximum temperature of the hottest month (ºC)	35.2	16.3	30.6	35.3	40.0	14.3- 45.0
Mean annual precipitation (mm)	1143.7	46.8	760.9	1093.2	1492.0	9.7- 4182.2
Minimum precipitation in the driest month (mm)	11.7	151.6	1.0	4.4	14.9	0.0- 165.6
Maximum precipitation in the wettest month (mm)	241.6	45.4	162.7	227.5	307.5	6.3- 840.1
Total precipitation in the rainy season (mm)	916.4	62.6	501.5	904.8	1290.4	0.0- 4129.1
Dry months (< 100 mm of precipitation per month) (number)	7.4	32.7	6.0	7.0	9.0	0.0- 12.0
Months under hydric stress (number)	4.4	62.8	2.0	5.0	6.0	0.0- 12.0
Lang aridity index	41.0	53.3	25.4	38.1	53.3	0.3- 151.8

Soil						
Depth (m)	2.1	60.0	1.3	1.8	2.6	0.1- 8.0
Bulk density[1] (g cm^{-3})	1.5	9.3	1.4	1.5	1.5	0-1- 2.0
Coarse fragments[1] (%)	13.8	69.6	7.0	12.0	19.0	0.0- 61.0
Clay content[1] (%)	35.5	23.3	31.0	37.0	41.0	2.0- 63.0
Field capacity[1] (mm)	409.3	9.6	392.6	413.8	430.3	100.0-807.4
Water holding capacity[1] (mm)	360.7	52.2	234.0	330.0	418.0	20.0- 650.0
pH[1] (H_2O)	6.4	12.4	5.8	6.3	6.9	4.6- 9.0
Cation exchange capacity[1] (cmol$_c$ kg^{-1})	18.7	41.7	13.5	18.4	22.8	2.2- 64.3
Organic carbon[1] (Mg ha^{-1})	73.6	87.5	38.4	58.7	78.5	2.2- 690.8
Total nitrogen[1] (g m^{-2})	914.6	66.3	289.6	921.3	1348.8	1.6- 3388.8
Total phosphorus[2] (g m^{-2})	437.8	69.1	272.4	321.9	503.8	45.0- 1576.8

Note. [1], soil depth 0-1.0 m; [2], soil depth 0-0.5 m.

Table S3. Correlates of spatial variation in soil fertility properties with climate in tropical dry forest ecoregions.

Climate metric	**Soil properties**	***r* value**	***p* value**
Minimum temperature	pH	0.363	< 0.001
	CEC	0.172	< 0.001
	Organic C	-0.048	< 0.001
	Total N	-0.013	0.279
	Total P	0.143	< 0.001
Maximum temperature	pH	0.417	< 0.001
	CEC	0.120	< 0.001
	Organic C	-0.189	< 0.001
	Total N	-0.091	< 0.001
	Total P	0.070	< 0.001
Precipitation in the driest month	pH	-0.177	< 0.001
	CEC	0.113	< 0.001
	Organic C	0.424	< 0.001
	Total N	0.275	< 0.001
	Total P	0.215	< 0.001
Precipitation in the wettest month	pH	-0.349	< 0.001
	CEC	0.108	< 0.001
	Organic C	0.127	< 0.001
	Total N	0.069	< 0.001
	Total P	0.067	< 0.001
Total precipitation in the rainy season	pH	-0.557	< 0.001
	CEC	-0.037	0.002
	Organic C	0.279	< 0.001
	Total N	0.123	< 0.001
	Total P	0.055	< 0.001

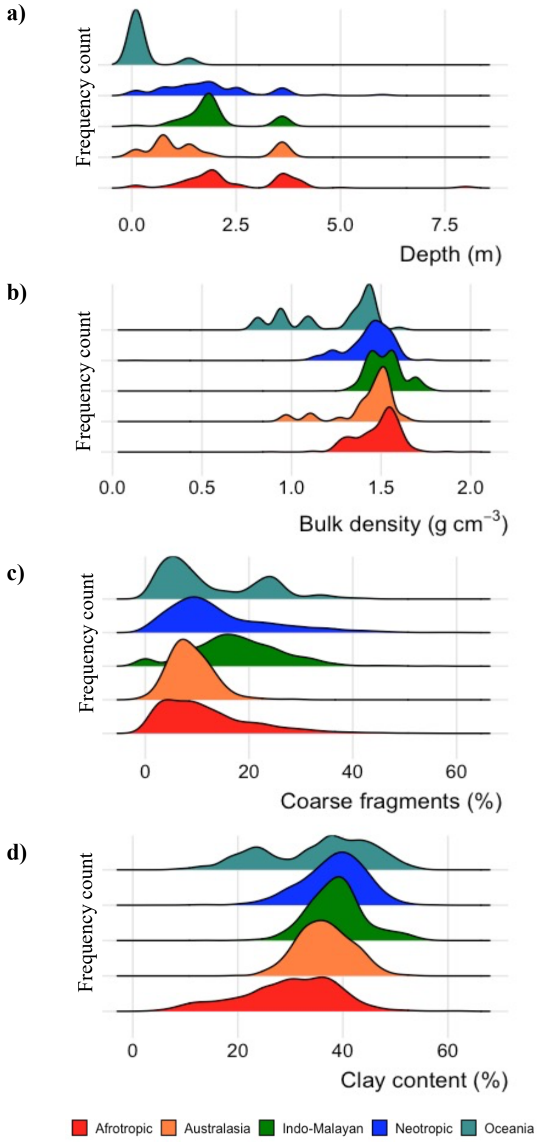

Figure S1. Variation in soil physical properties within and amongst biogeographic regions.

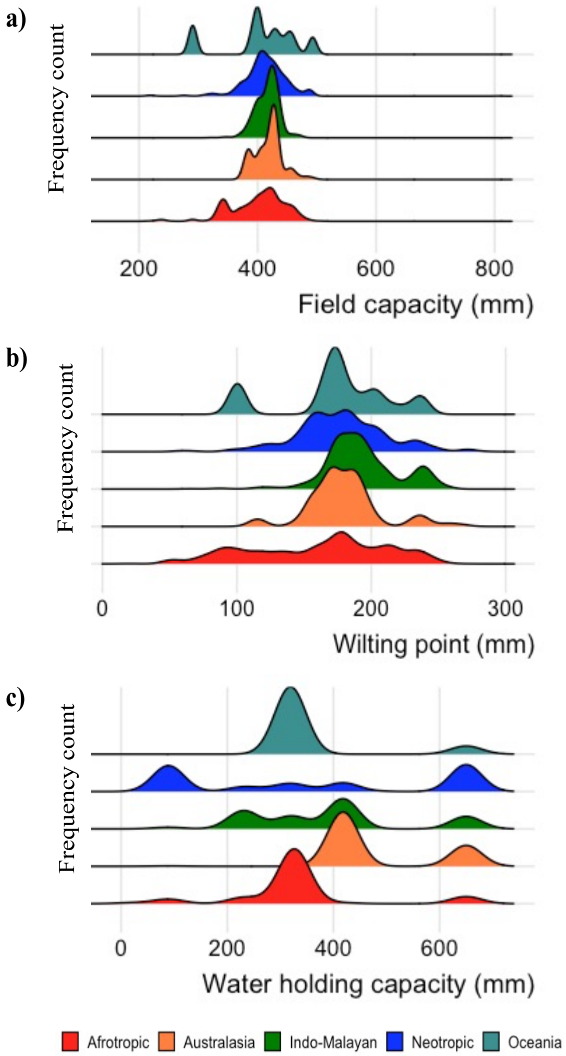

Figure S2. Variation in soil water retention properties within and amongst biogeographic regions.

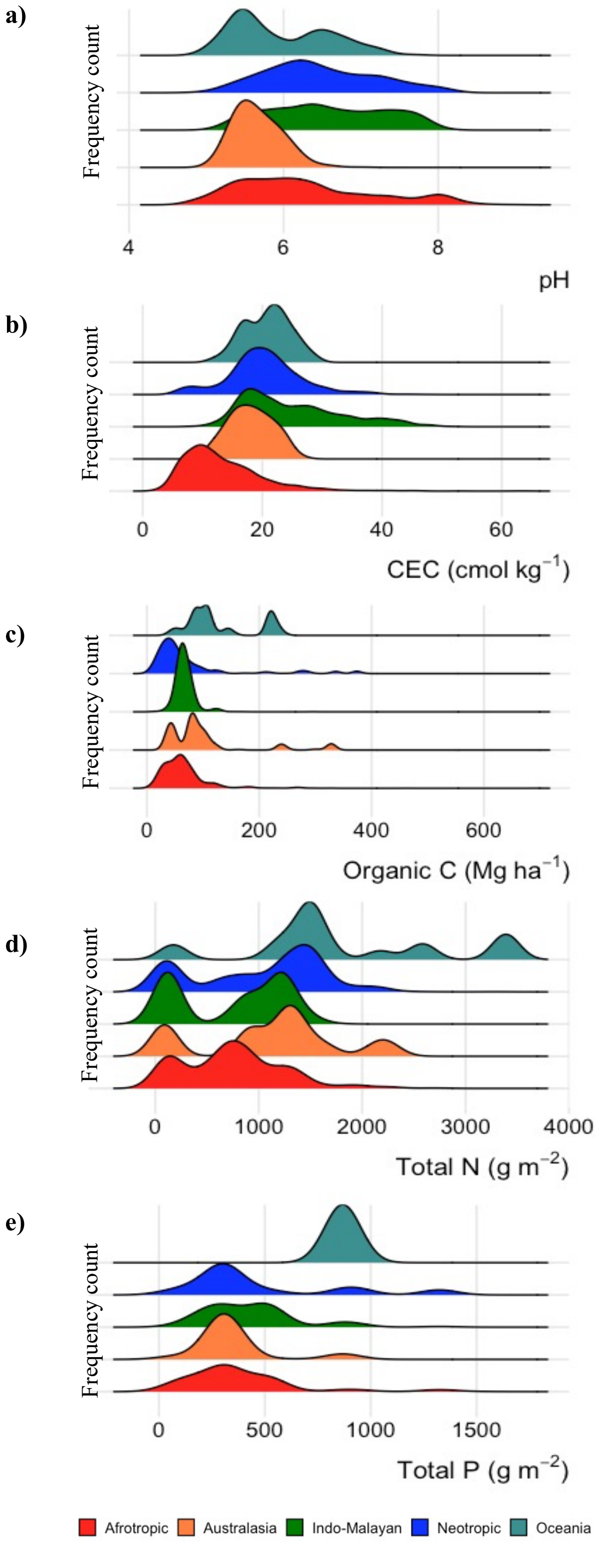

Figure S3. Variation in soil fertility properties within and amongst biogeographic regions.

Capítulo II

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Artículo de requisito

Differences in nitrogen cycling between tropical dry forests with contrasting precipitation revealed by stable isotopes of nitrogen in plants and soils

Anaitzi Rivero- Villar, Pamela H. Templer, Víctor Parra-Tabla, and Julio Campo

Resumen

A pesar del vínculo conocido entre el clima y el ciclo biogeoquímico del N en bosques tropicales, la información fundamental del ciclo del N es incompleta aún. Nuestro objetivo fue establecer las diferencias en el ciclo del N entre dos bosques tropicales secos bajo regímenes de precipitación contrastantes (1240 o 642 mm de lluvia anual media). Para ello, examinamos una métrica de corto plazo del ciclo de N (la concentración de N) y una métrica más integrada del ciclo (la abundancia natural de ^{15}N) en plantas y suelos en ambos sitios. En ambos, el relativamente húmedo y el seco, el ciclo del N asociado con dos especies no fijadoras de N_2 fue comparado con el ciclo del N asociado con dos especies potencialmente fijadoras de N_2; las cuatro especies de árboles consideradas fueron dominantes en ambos sitios. La abundancia de ^{15}N en las plantas fue mayor en el sitio con poca lluvia, presentando que las pérdidas de N desde el sistema puede que sean grandes. En contraste, las métricas de N a corto plazo no variaron con la lluvia. Aunque existió una tendencia a una concentración elevada de N en hojas de los árboles que tienen asociaciones potenciales con fijadores de N_2, solamente el ^{15}N en el piso forestal fue significativamente mayor bajo árboles con dosel de contenido elevado de N (especies fijadoras de N_2) que en aquellos con contenido bajo de N (especies no fijadoras de N_2). En cada sitio, la influencia de las especies fijadoras de N_2 en el ciclo del N aumentó con la disminución en la lluvia. En general, nuestros resultados demuestran el papel del clima como un control del ciclo de N en la región, tal que la disminución proyectada en la precipitación para esta región puede conducir a mayores pérdidas de N en estos bosques. Este estudio presenta también como cambios en las especies de árboles con y sin asociaciones para fijar el N_2 pueden impactar en el ciclo del N de los bosques tropicales secos en un futuro.

Palabras clave: Cambio climático, N hoja, Especies fijadoras de N

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Differences in nitrogen cycling between tropical dry forests with contrasting precipitation revealed by stable isotopes of nitrogen in plants and soils

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ABSTRACT

Despite the known links between climate and biogeochemical cycling of N in tropical forests, fundamental knowledge of N cycling is still far from complete. Our objective was to ascertain differences in the N cycle of two tropical dry forests under contrasting precipitation regime (1240 or 642 mm of mean annual rainfall). To do so, we examined a short-term metric of N cycling (N concentration) and a more integrated metric of N cycling (natural abundance ^{15}N) in plants and soils at both sites. At both the relatively wet and dry sites, N cycling associated with two non-N_2-fixing species was compared to N cycling associated with two potential N_2-fixing species; all four tree species considered were dominant at both sites. The ^{15}N abundance in plants was highest in the site with low rainfall, showing that N losses from the system may be large. By contrast, short-term N metrics did not vary with rainfall. Although there was a trend for leaf N concentration to be elevated in trees that have potential associations with N_2-fixers, only ^{15}N in the forest floor was significantly greater under trees with high canopy N (N_2-fixing species) than those with low canopy N (non-N_2-fixing species). Within each site, the influence of N_2-fixing species on N cycling increased with a reduction in rainfall. Overall, our results demonstrate the role of climate as a driver of N cycling in the region, such that the projected decrease in precipitation in this region may lead to larger N losses in these forests. This study also shows how changes in tree species with and without N_2-fixing associations may impact N cycling in tropical dryland forests in the future.

Abstract in Spanish is available with online material.

Key words: climatic change; leaf N; Mexico; N_2-fixing species.

Soil nitrogen (N) availability limits net primary productivity across a wide variety of tropical forests (LeBauer & Treseder 2008, Fisher *et al.* 2012, Bejarano-Castillo *et al.* 2015). Despite the importance of the N limitation for tropical forest function, fundamental uncertainties remain about N cycling. For example, it is not well understood how N dynamics at the ecosystem level will respond to changes in global climate (Allen *et al.* 2017). Rapid climate change, with consequences for ecosystem processes, underscores the urgent need to elucidate how biogeochemical cycles will respond (Cavaleri *et al.* 2015). Moreover, evidence from many tropical humid regions points to a link between lower amounts of annual precipitation and an increase in N content in leaves and soil, suggesting that precipitation regime-driven shifts in plant–soil feedbacks may limit litterfall N inputs from vegetation to the soil, and thus may have large impacts on N availability in soils (Martinelli *et al.* 1999, Nardoto *et al.* 2008).

Here, we focus on N cycling in tropical dry forests (TDFs) where there is both direct and indirect evidence that both water and N availability constrain net primary productivity and carbon accumulation at the ecosystem level (Campo & Vázquez-Yanes 2004, Campo 2016, Corona-Núñez *et al.* 2018). Despite this evidence, as far as we know, the links between water availability, soil nutrient availability, and plant N acquisition are limited. The possible modifications of N cycling in TDFs in response to changes in rainfall regimes are significant at a global scale for two reasons. First, TDFs cover approximately 42 percent of the total area of tropical forest biome (Murphy & Lugo 1986) and are expected to experience a decrease in mean annual precipitation (MAP) over the coming century (Miles *et al.* 2006). Second, evidence suggests that N limitation will become dominant and more intense in areas where climate change intensifies water limitation (Delgado-Baquerizo *et al.* 2016, Augusto *et al.* 2017).

There are many proxies for studying nutrient cycling in ecosystems. We employed stable isotope techniques, which constitute a powerful tool for elucidating controls on N cycling processes and have provided a basis for key insights into biogeochemical interactions among soil, plants, and the atmosphere (Dawson *et al.* 2002, Almaraz & Porder 2016). The internal transformations of N involve several isotopic fractionation processes, discriminating against the heaver ^{15}N stable isotope when chemical bonds are broken and causing the product of a

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particular biological process to have greater abundance of the lighter isotope, ^{14}N, relative to the heavy isotope, ^{15}N (Mariotti *et al.* 1981, Robinson 2001). If rates of a biological process such as nitrification increase and some of the nitrate produced is lost via leaching or denitrification, the remaining nitrate in soils is depleted in ^{15}N relative to the ammonium substrate, but can become enriched in ^{15}N over time as the lighter ^{14}N is lost from the ecosystem. Therefore, in ecosystems with relatively high rates of nitrification and nitrate loss, the remaining N pools in soil and plants become enriched in ^{15}N over time (Nadelhoffer & Fry 1994). Several studies have revealed a positive relationship between soil N availability and nitrification and mineralization rates with soil, foliar, and root δ^{15}N values at the community and ecosystem levels (Schmidt & Stewart 2003, Pardo *et al.* 2006, Craine *et al.* 2009). Further, ecosystems that have a relatively 'open' N cycle with high internal N cycling rates (*e.g.*, nitrification) and N losses typically have vegetation, soils, and inorganic N pools that are enriched in ^{15}N relative to more closed ecosystems with lower rates of N cycling and loss (Amundson *et al.* 2003, Craine *et al.* 2015a). It has been observed that natural abundance ^{15}N (hereafter referred to as δ^{15}N) varies systematically along climatic gradients, with lower values associated with greater rates of precipitation (Amundson *et al.* 2003, Craine *et al.* 2015b). The isotopic fractionation that occurs during the uptake of soil N varies among plants and depends on soil N availability and on the association with N_2-fixing bacteria (Craine *et al.* 2009, 2015b).

Climate models estimates that by the end of the 21st century, the region of the Yucatan Peninsula, Mexico will experience long-term rainfall decreases of more than 50 percent (Chadwick *et al.* 2016). This rainfall shift could have large effects on the biogeochemistry of the water-limited ecosystems of the region, as the TDFs. In this study, we aimed to ascertain differences in the N cycle in two TDFs of the Yucatan Peninsula that receive different amounts of mean annual rainfall (1240 or 642 mm of annual rainfall). To do so, we examined N concentration and δ^{15}N in plant leaves and roots and in soils (forest floor and mineral soil) at both sites. These two sites were chosen because the wetter condition represents the average rates of rainfall around large parts of Yucatan Peninsula, and the drier site represents the amount of rainfall projected to occur over the next century (Conde *et al.* 2011, Chadwick *et al.* 2016). Similarly, in view of the influence of canopy chemistry on the soil, N cycling associated with two plant species with potential N_2-fixing associations was compared to N cycling associated with two non-N_2-fixing species; all four tree species considered were dominant at both sites. The metrics analyzed provided insights into short-term proximal N source measured by concentrations of extractable mineral N (*i.e.*, nitrate and ammonium) and integrated controls on the N cycling indicated by δ^{15}N in vegetation and soils (see Amundson *et al.* 2003, Houlton *et al.* 2007, Osborne *et al.* 2017). The advantage to using this study system is that potential differences in N cycling due to altitude, air temperature, parent material, and vegetation type (TDF) were excluded as the two forests have minimal differences in these topographic and climatic characteristics, and both developed on similar parent material.

Average soil moisture content decreases and water deficit increases from south to north across the region (Roa-Fuentes *et al.* 2012), resulting in a decrease in plant biomass and net primary productivity along the south to north gradient of Yucatec TDFs (Campo & Merino 2016). We hypothesized that differences in water availability affect N cycling in these forests. Specifically, we hypothesized that (1) soil N availability is lower in sites with lower MAP; (2) the lower amount of MAP results in a decoupling of plant N demand and N supply, leading to a more open N cycle and isotopic enrichment of plant and soil N; and (3) within a site, soil N availability is higher with trees with potential N_2-fixing symbionts than under trees with no N_2-fixers.

METHODS

STUDY SITES.—The study was carried out at two sites with different precipitation regimes on the Yucatan Peninsula, Mexico. The sites contrast in MAP: the drier, semiarid, site in the north receives approximately half the total annual precipitation received at the wetter, subhumid, southern site (Table 1).

Long-term climate data from Mexico National Weather Service show that both sites are characterized by a distinct period of low precipitation (5–7 mo with precipitation below 100 mm per month; Table 1). Across the sites, variation in mean annual temperature is <1°C, and the climate, semiarid to subhumid, support

TABLE 1. *Characteristics of the forest sites.*

	Semiarid site	Subhumid site
Coordinates	21°12′ N, 89°36′ W	20°04′ N, 88°02′ W
Altitude (m asl)	8	36
Climate	BS1	Aw1
Mean annual temperature (°C)[a]	25.4	25.5
Mean annual precipitation (mm/yr)[a]	642	1240
Potential evapotranspiration (mm/yr)[a]	1713	1719
Annual ratio of precipitation to potential evapotranspiration	0.37	0.72
Mean monthly precipitation in the dry season (mm/yr)[a]	30.2	42.6
Soil (0–10 cm)[b]		
Bulk density (g/cm^3)	0.61	0.84
Clay (%)	26	64
pH	8.1	7.5
Organic C (mg/g)	222	59
Vegetation[c]		
Aboveground biomass (Mg/ha)	47.4	65.6
Total root biomass (Mg/ha)	22.1	19.3

[a] Mexico National Weather Service- CONAGUA.

[b] Roa-Fuentes *et al.* (2015).

[c] Roa-Fuentes *et al.* (2012).

both tropical very dry or dry forest in the Holdridge life zone system (Holdridge *et al.* 1971).

The two sites both have consistently flat terrain, with <50 m of altitudinal variation between them (Table 1). Soils in the Yucatan Peninsula are derived from Tertiary limestone in a typical karstic landscape of flat rock outcrops and shallow depressions (Bautista *et al.* 2011), and generally fall into two groups: shallow black soils (*Lithic Usthortens*) surrounding rock outcrops, and deeper red soils (*Lithic Haplustolls*) at slightly lower relief. Soils at the semiarid site are mainly black soils; with increased MAP there is also an increase in the cover area of red soils, which are the predominant soils at the subhumid site. At the semiarid sites, the pH of the soils is higher, and soils are less dense due to the greater amount of soil organic matter **(**Campo & Merino 2016**)**, compared to the subhumid site (Table 1). Soil water retention increases with rainfall, from 33 percent of field capacity at the semiarid site to 66 percent of field capacity at the subhumid site **(**Roa-Fuentes *et al.* 2012**)**, reflecting changes in soil clay content.

The predominant ecosystem type at both study sites is TDF. Mean canopy height is low due to hurricanes, which are an important part of the natural disturbance regime throughout the Yucatan Peninsula (Mascorro *et al.* 2016). Tree height decreases with decrease in MAP from 5.4 m at the subhumid site to 3.3 m at the semiarid site **(**Roa-Fuentes *et al.* 2012**)**. The subhumid site has more trees (diameter at breast height, dbh $\geq$ 2.5 cm) with 3900 ± 305 (mean ± 1 SE) trees per hectare versus 2600 ± 300 trees/ha at the semiarid site. Floristically, *Fabaceae* is the most abundant plant family at both forest sites and the relative basal area of these trees increase from 10.8 ± 1.7 percent in the subhumid site to 64.7 ± 6.0 percent in the semiarid site (A. Rivero-Villar, unpubl. data). The most abundant leguminous tree species in both sites are *Lysiloma latisiliquum* (L.) Benth and *Piscidia piscipula* (L.) Sarg; other abundant *Fabaceae* are *Acacia gaumeri* Blake, *Leucaena leucocephala* Wit, *Mimosa bahamensis* Benth, and *Pithecellobium dulce* (Roxb.) Benth.

FIELD SAMPLING.—Two field campaigns were conducted, one in the rainy season to collect leaves and fine root samples, and the other in the following dry season to collect both forest floor and mineral soil samples. In the first campaign (September 2014 in the rainy season), 80 mature trees (dbh $\geq$5 cm) (10 trees per plot) were randomly chosen in eight plots (12 m × 12 m of size) (with 8 m buffers between each plot) in each site for leaves and fine root sampling, to provide insight into plant N dynamics in forest communities. A second set of samples of leaves and fine roots from dominant canopy species (two non-N_2-fixing species, *Bursera simaruba* (L.) Sarg., *Burseraceae*, and *Gymnopodium floribundum* Rolfe, *Polygonaceae*; and two potential N_2-fixing species, *Lysiloma latisiliquum* (L.) Benth and *Piscidia piscipula* (L.) Sarg, *Fabaceae* was taken in this campaign; eight mature trees of each species were sampled per site (one per plot), making a total of 64 trees sampled per site), to explore the influence of tree species with and without N_2-fixing associations on N cycling. In both samplings, mature leaves from ten fully sunlit branches (haphazardly retrieved from all parts of the canopy) were collected. Also, in this sampling, four mineral soil samples (0–10 cm in depth) were taken around each stem at a distance of 15 cm for collect fine roots. These soil samples were combined into a composite sample per tree and used only for the analysis of fine root (<2 mm diameter) N after sieving (2 mm in mesh). The soils were discarded. All the target tree species are deciduous and are henceforth referred to by genus name only.

The second campaign took place in May 2015 (at the end of the dry season) and focused on forest floor and mineral soil sampling for N analysis. We sampled forest floor and mineral soils during the dry season since soil nutrients often accumulate in the forest floor and the mineral soil layers due to low rates of leaching and plant uptake in TDFs during the rainless period (Gei & Powers 2014). Twelve surface forest floor samples were collected from each of the eight plots (96 samples total) per site. The forest floor samples contained only dead plant material, including freshly fallen litter and the more finely decomposed litter fraction. The samples were randomly collected, and at each point, a mineral soil sample (0–10 cm in depth) was also taken. Both forest floor and mineral soil samples were combined in the field in composite samples of each per plot. We took a second set of samples of forest floor and soil (from the first 10 cm of the soil profile) focusing on dominant tree species. Four independent forest floor and soil samples were taken adjacent to each tree of each dominant species, at 15 cm around the trunk and compositing them for each tree. All soil samples were stored at 4°C until processing.

ANALYTICAL METHODS.—In the laboratory, fresh leaves were removed from the petiole, and roots were washed with deionized water. Soil samples were homogenized and sieved using a 2-mm mesh. All samples were oven-dried at 60°C to constant weight for 48 h, and then ground in an agate mortar to obtain a fine powder. Natural abundance ^{15}N analysis was carried out in the Stable Isotope Laboratory of Boston University, where samples were combusted in a Euro EA elemental analyzer and the combustion gases were separated into a gas chromatography column, passed through a GV Instruments diluter and reference gas box, and analyzed for ^{15}N content using a GVI IsoPrime isotope ratio mass spectrometer.

Soils were extracted with 50 mL of 2 M KCl (Robertson *et al.* 1999), shaken for 1 h, and allowed to settle overnight (8 h). A 20-mL aliquot supernatant was transferred to sample vials and frozen for later analysis. The analysis was performed with an autoanalyzer system using procedures for NO_3–N + NO_2–N determination, reported as NO_3–N, and the salicylate–hypochlorite procedure for NH_4–N. The concentration of total soil N was determined from acid digestion in H_2SO_4 concentrated (Anderson & Ingram 1993) using a NP elemental analyzer (Technicon Autoanalyzer).

DATA ANALYSIS.—Potential differences in N concentration and ^{15}N natural abundance in the leaves, roots, forest floor, and inorganic forms between sites were tested with one-way ANOVA. Nitrogen concentration of leaves was transformed logarithmically before analysis because data were not normally distributed. For δ^{15}N in leaves and roots, we performed a Kruskal–Wallis test (*H*), because the data were not normally distributed. Within each site, we performed one-way ANOVA between non-N-fixing species and N-fixing species per site. The differences between sites were tested with a nested ANOVA, in which the fixed factor was the site and the plant functional group was nested within site. For all analyses, a significance level of $P < 0.05$ was used. Statistical analyses were conducted in R 3.3.1 (R Development Core Team 2016).

RESULTS

VARIATION IN N CYCLING BETWEEN SITES.—Nitrogen concentration in leaves, roots, forest floor, and soil (total N) differed significantly between sites, with the lowest concentrations in the site with the greater amount of MAP (Table 2; $F = 7.70–118.7$, $P < 0.05$ for all ecosystems pools). In contrast, there were no significant differences in concentrations of soil NO_3^- and NH_4^+ or ratios of NO_3^- -N: NH_4^+ -N ($F = 0.001–2.22$, $P > 0.05$).

^{15}N natural abundance in leaves and roots differed considerably between sites by a factor of two following the pattern of changes in N concentration between sites detected for plant organs (*i.e.*, higher δ^{15}N value at site with lower MAP; Table 2; $H = 75.0$ for leaves, and $H = 60.6$ for roots; $P < 0001$). Consistently, the semiarid site plants had wider δ^{15}N ranges (0.42 to 8.16‰ for leaves, and −0.35 to 5.16‰ for roots) compared to those of the subhumid site (−0.41 to 4.69‰ and −1.24 to 2.99‰, for leaves and roots, respectively; $P < 0.01$ when comparing the range of values across the two sites for both leaves and roots). Similarly, ^{15}N abundance in both forest floor and mineral soil layers were greater in the site with lower amounts of MAP ($F = 120.5$ for the forest floor, and $F = 20.6$ for the mineral soil N; $P < 0001$).

TABLE 2. *Nitrogen concentration and ^{15}N natural abundance in leaves, roots, forest floor and soil (0–10 cm in depth) in tropical dry forests at Yucatan Peninsula.*

	Semiarid site (642 mm/yr)	Subhumid site (1240 mm/yr)
Leaf N (mg/g)	30.3 ± 0.8	25.1 ± 0.6
Root N (mg/g)	26.6 ± 0.5	20.7 ± 0.4
Forest floor N (mg/g)	23.8 ± 0.4	16.9 ± 0.5
Soil total N (mg/g)	28.5 ± 1.7	22.7 ± 1.4
Soil NH_4^+ (μg/g)	16.4 ± 1.9	16.4 ± 1.4
Soil NO_3^- (μg/g)	9.53 ± 1.3	11.6 ± 0.7
Soil NO_3^- : NH_4^+ ratio	0.61 ± 0.01	0.78 ± 0.09
Leaf δ^{15}N (‰)	4.83 ± 0.2	2.04 ± 0.10
Root δ^{15}N (‰)	2.69 ± 0.13	1.18 ± 0.09
Forest floor δ^{15}N (‰)	4.23 ± 0.25	0.92 ± 0.21
Soil δ^{15}N (‰)	7.24 ± 0.40	5.29 ± 0.23

Nitrogen values in the forest floor, and total N, NH_4^+ and NO_3^- values in the soil are means ± 1 SE ($n = 8$); leaf and root values are means ± 1 SE ($n = 80$).

VARIATION IN N CYCLING AMONG DOMINANT SPECIES ACROSS SITES.—Generally, N concentrations and ^{15}N natural abundance in trees and soils (both forest floor and mineral soil layers) did not vary between the two potential N_2-fixing species (*Lysiloma* and *Piscidia*) or between the non-N_2-fixing species (*Bursera* and *Gymnopodium*) within each site (Table 3; $P > 0.05$). At the semiarid site, exceptions were observed between potential N_2-fixing species; leaves of *Lysiloma* had greater concentrations of N and abundance of ^{15}N natural than leaves of *Piscidia* ($F = 46.6$, $P < 0.001$ for N concentration, and $F = 5.51$, $P < 0.05$ for δ^{15}N). In addition, forest floor was enriched in ^{15}N beneath *Lysiloma* compared to forest floor beneath *Piscidia* ($F = 16.6$, $P < 0.001$). NO_3 concentrations were higher in soils beneath *Piscidia* than in soils beneath *Lysiloma* ($F = 14.1$, $P < 0.001$). In contrast to potential N_2-fixing species, N concentrations and ^{15}N natural abundance in plants and soils did not vary between non-N_2-fixing species at this site.

The differences in N concentrations and in ^{15}N natural abundance between potential N_2-fixing species detected in plants at the semiarid site was not observed in those of the subhumid site (Table 3). In addition, N concentrations and ^{15}N natural abundance in the forest floor and mineral soils did not vary among species ($P > 0.05$). In contrast, N concentrations were greater in leaves of *Bursera* than in leaves of *Gymnopodium* ($F = 7.63$, $P < 0.05$) and ^{15}N abundance in leaves was greater in *Gymnopodium* than in *Bursera* ($F = 14.2$, $P = 0.001$). Also, ^{15}N abundance was greater in the forest floor under *Gymnopodium* than in the floor under *Bursera* ($F = 4.38$, $P < 0.05$).

Trees of the potential N_2-fixing group had greater N concentrations in leaves and roots than those in the non-N_2-fixing group, largely reflecting differences in N attributes between leguminous and non-leguminous trees (Table 3; see *Site : Functional group* nested analyses in Table 4). The nested ANOVA test shows that non-N_2-fixing plants consistently had greater levels of ^{15}N in leaves and roots than potential N_2-fixing plants. The patterns for N concentrations and ^{15}N abundance observed in leaves and roots were not reflected in the forest floor and mineral soil; neither N concentration nor ^{15}N abundance exhibited significant variation across functional groups.

As with regional variability, N concentrations and δ^{15}N in target tree species and soils displayed a marked change across sites with lower values in the site with greater precipitation compared to lower precipitation (see *Site effect* in Table 4).

DISCUSSION

Many tropical dry regions are predicted to experience droughts with increasing frequency and intensity over this century (IPCC 2013, Chadwick *et al.* 2016); since this change in climate will likely alter the functions of this tropical ecosystem (Allen *et al.* 2017), we sought to contribute to the understanding of how N

TABLE 3. *Nitrogen concentration and ^{15}N natural abundance in leaves, roots, and in forest floor and soil (0–10 cm in depth) beneath dominant non-N_2-fixing species (Bursera and Gymnopodium) and potential N_2-fixing species (Lysiloma and Piscidia) in tropical dry forests at Yucatan Peninsula.*

	Bursera	*Gymnopodium*	*Lysiloma*	*Piscidia*
Semiarid site (642 mm/yr)				
Leaf N (mg/g)	18.9 ± 0.4	16.3 ± 1.1	30.4 ± 0.4	26.0 ± 0.5
Root N (mg/g)	17.3 ± 0.9	15.0 ± 2.3	22.3 ± 1.6	24.5 ± 1.2
Forest floor N (mg/g)	20.0 ± 1.1	22.0 ± 0.7	22.4 ± 0.7	21.4 ± 0.4
Soil total N (mg/g)	31.7 ± 1.9	30.4 ± 0.9	31.3 ± 1.0	28.8 ± 1.1
Soil NH_4^+ (μg/g)	17.0 ± 1.9	17.8 ± 2.1	18.0 ± 2.6	16.4 ± 1.8
Soil NO_3^- (μg/g)	6.3 ± 1.3	7.5 ± 1.3	6.1 ± 1.4	11.9 ± 0.8
Soil NO_3^- : NH_4^+ ratio	0.37	0.42	0.34	0.73
Leaf δ^{15}N (‰)	5.50 ± 0.38	5.26 ± 0.35	3.91 ± 0.22	2.86 ± 0.41
Root δ^{15}N (‰)	2.79 ± 0.36	2.30 ± 0.31	1.55 ± 0.25	1.78 ± 0.27
Forest floor δ^{15}N (‰)	3.81 ± 0.22	4.18 ± 0.25	4.21 ± 0.18	3.31 ± 0.15
Soil δ^{15}N (‰)	6.52 ± 0.36	6.85 ± 0.31	6.55 ± 0.17	6.29 ± 0.21
Subhumid site (1240 mm/yr)				
Leaf N (mg/g)	18.4 ± 1.2	15.5 ± 1.0	22.2 ± 1.3	23.1 ± 0.9
Root N (mg/g)	16.4 ± 1.6	15.7 ± 1.1	18.9 ± 1.3	18.9 ± 1.5
Forest floor N (mg/g)	19.5 ± 0.7	20.4 ± 0.8	20.6 ± 1.1	21.0 ± 07
Soil total N (mg/g)	16.6 ± 1.2	15.6 ± 1.1	19.9 ± 1.4	18.6 ± 1.7
Soil NH_4^+ (μg/g)	17.0 ± 3.9	12.1 ± 2.7	16.8 ± 4.0	18.0 ± 3.0
Soil NO_3^- (μg/g)	11.4 ± 2.1	7.2 ± 1.4	11.4 ± 2.1	11.9 ± 2.5
Soil NO_3^- : NH_4^+ ratio	0.67	0.59	0.68	0.66
Leaf δ^{15}N (‰)	1.27 ± 0.21	2.88 ± 0.32	2.05 ± 0.44	1.74 ± 0.25
Root δ^{15}N (‰)	1.08 ± 0.26	1.47 ± 0.20	0.19 ± 0.32	0.24 ± 0.42
Forest floor δ^{15}N (‰)	1.98 ± 0.14	2.42 ± 0.17	1.89 ± 0.20	1.67 ± 0.23
Soil δ^{15}N (‰)	4.49 ± 0.32	4.28 ± 0.24	3.47 ± 0.56	4.04 ± 0.52

Values are means ± 1 SE (n = 10).

cycling in TDFs may be sensitive to differences in precipitation regime.

REGIONAL VARIATION IN N CYCLING.—Contrasting precipitation regimes had a strong influence on leaf and root N concentrations. Low amounts of rainfall can drive an increment in leaf and fine root N concentrations, despite reduced decomposition rates (Bejarano *et al.* 2014, Campo & Merino 2016) that can, in turn, slow rates of N recycling between microbial and vegetation (Campo 2016). The low water availability and decomposition rates (Bejarano *et al.* 2014) results in accumulation of N in the forest floor (by an increase in N concentration in forest floor and mineral soils, Table 2; and an increase in forest floor mass, Campo 2016). Our results (Table 2) suggest that leguminous plants under semiarid conditions are associated with greater N concentrations in leaves that could compensate for the expected low photosynthetic rates induced by reduced stomatal conductance (Wright *et al.* 2003, Santiago *et al.* 2017) that may result in lower rates of N uptake by trees, and in roots to enhance root metabolism and growth for the uptake of soil nutrients and water (Sardans *et al.* 2017). Moreover, plants at the semiarid site allocated more resources to roots (root to total biomass proportion increase from 0.23 to 0.32 with decreased MAP; Roa-Fuentes *et al.* 2012). Thus, our data indicate differences in resource investment strategies for plants, in this case root biomass, as would be expected under an 'optimal partitioning theory' (Gedroc *et al.* 1996).

Our first hypothesis, that N availability would be lower at the semiarid site than at subhumid site, was not supported by differences in soil δ^{15}N or by inorganic N concentrations in mineral soil. Contrary to our hypothesis, we saw no differences in inorganic N concentrations in soils. On the other hand, our soil δ^{15}N data suggest that regional variation in MAP creates differences in N cycling. For example, the pattern of increased foliar δ^{15}N and root δ^{15}N with lower rates of rainfall suggests that the semiarid site has a more open N cycle, in which N inputs and outputs are more important than intra-system cycling. These results support the conclusion that aridity results in increased openness of N cycling in tropical forests due to greater losses in dry ecosystems, compared to the more efficient N cycling in wetter ecosystems (Ometto *et al.* 2006, Soper *et al.* 2015). This openness, which leads to soil ^{15}N enrichment and hence plant ^{15}N enrichment as well, is likely driven in part by reduced plant N demand (around 27% lower than in the subhumid site; Campo 2016) due to relatively lower net primary productivity (Campo & Merino 2016) as well as other factors, such as limitation by water

TABLE 4. *Functional group nested within site effects on nitrogen concentrations and ^{15}N natural abundance of dominant non-N$_2$-fixing and potential N$_2$-fixing tree species in tropical dry forests at Yucatan Peninsula.*

Variable	Source of variation	*F*	*P*
Leaf N	Site	19.8	<0.001
	Site: Functional group	6.18	0.003
Root N	Site	14.5	<0.001
	Site: Functional group	0.761	0.467
Forest floor N	Site	3.94	0.050
	Site: Functional group	1.33	0.271
Soil total N	Site	205	<0.001
	Site: Functional group	1.36	0.149
Soil NH_4^+	Site	0.521	0.473
	Site: Functional group	0.605	0.549
Soil NO_3^-	Site	10.3	0.001
	Site: Functional group	0.733	0.483
Soil NO_3^- : NH_4^+ ratio	Site	9.78	0.002
	Site: Functional group	0.563	0.571
Leaf δ^{15}N	Site	108	<0.001
	Site: Functional group	17.0	<0.001
Root δ^{15}N	Site	44.7	<0.001
	Site: Functional group	11.4	<0.001
Forest floor δ^{15}N	Site	176	<0.001
	Site: Functional group	2.84	0.064
Soil δ^{15}N	Site	106	<0.001
	Site: Functional group	2.33	0.142

due to more extended and frequent rainfall shortages. Hydrologic N losses by leaching are unlikely to occur since this path of N output from the ecosystem is not accompanied by fractionation (Craine *et al.* 2015a). Therefore, gaseous losses in the dry site appear primarily responsible for causing enrichment of ^{15}N in plants and ecosystems (Houlton & Bai 2009), particularly in the tropical forests we examined. Significant ^{15}N enrichment of soil N pools can be expected under high rates of N gaseous loss due to fractionation of ^{15}N during nitrification and denitrification (Mariotti *et al.* 1981, Martinelli *et al.* 1999, Robinson 2001, Houlton & Bai 2009). Previous research has documented increasing plant δ^{15}N and soil δ^{15}N in tropical dry regions caused by increased gaseous losses of isotopically light N with decreased rainfall (Viani *et al.* 2011, Roa-Fuentes *et al.* 2015). The scarcer rainfall and its concentration into a shorter period at the semiarid site, as compared to its subhumid counterpart, possibly leads to a mismatch between the time when most of the N is mineralized by soil microbes and the time of the highest N uptake by plants (Saynes *et al.* 2005).

Areas with low δ^{15}N values (such as our subhumid site) may have closed cycles with fast immobilization or absorption of mineralized N or, alternatively, high losses compensated for by high rates of N$_2$ fixation. Although uncertainty about N fixation in the TDF of the subhumid site prevents determining which of the two patterns they follow, the lack of evidence of N$_2$ fixation in roots associated with trees suggests a high level of immobilization and/or absorption of mineralized N. Direct evidence from a field experiment with $^{15}NH_4$ and $^{15}NO_3$ additions indicates a large amount of N uptake by fine roots at our wetter site (J. Campo, unpubl. data). On the other hand, the low P availability at the semiarid site (Campo 2016) could result in high N losses and explain the high ^{15}N abundance. A recent study at these TDF sites did not observe differences in N resorption, though, consistent with the hypothesis of limited P availability; a high level of P resorption did occur at the drier site (León Aguilar 2017).

Finally, we did not find significant differences in leaf δ^{15}N between plants growing at the semiarid and subhumid sites when the background soil δ^{15}N is discounted from leaf δ^{15}N or root δ^{15}N ($\Delta\delta^{15}$N leaf – soil: −2.59 ± 0.22‰, mean ± 1 SE, for the semiarid site, and −3.25 ± 0.11‰ for the subhumid site) or root δ^{15}N ($\Delta\delta^{15}$N root – soil: −4.55 ± 0.13‰ and −4.11 ± 0.09‰ for the semiarid and subhumid sites, respectively). This lack of difference suggests that background soil differences in δ^{15}N are the main reason for differences in δ^{15}N in semiarid and subhumid plants. Nevertheless, it is difficult to assign a precise reason as to why there are similar δ^{15}N plant – soil enrichment factors at both sites, though it seems likely that this pattern reflects mainly the use of the same N sources at both sites.

Overall, our results suggest that precipitation regime largely influences soil N cycling in Yucatan forests over the long term, as indicated by integrators of the forest N cycle as observed in foliar and soil δ^{15}N (Craine *et al.* 2015b). Although the pattern in foliar ^{15}N indicates rainfall regime control, measurements of N availability (*e.g.*, inorganic N pools) did not vary across sites.

INFLUENCES OF POTENTIAL N$_2$-FIXING DOMINANT TREES ON N CYCLING.—Data from trees with potential N$_2$-fixing species in this analysis could also shed light on the sensitivity of the N cycle in TDF ecosystems to changes in rainfall regimes, due to the high abundance of legumes in the seasonally dry tropics (Pennington *et al.* 2006, Gei *et al.* 2018), and the effects of the group on the N cycling (Bustamante *et al.* 2004, Bai *et al.* 2009). Although this result could be due to the low rate of N fixation in TDF ecosystems (Nardoto *et al.* 2014, Ferreira da Silva *et al.* 2017), our data indicate that much of the variation in foliar N can be attributed to local conditions, particularly to rainfall regime, with little variation attributable to functional groups. Considering that the target potential N$_2$-fixing species and, in general, the legume group dominate forest biomass in the TDFs of Yucatan (Ceccon *et al.* 2002) and thus have a strong influence on N cycling, more intensive sampling is needed to obtain more conclusive evidence regarding the lack of these effects.

We also did not find significant differences in leaf δ^{15}N between plants with and without potential N$_2$-fixing species growing at the subhumid site. Moreover, differences were not significant when background soil δ^{15}N was discounted from leaf δ^{15}N ($\Delta\delta^{15}$N leaf – soil: −1.86 ± 0.44‰ for potential N$_2$-fixing, and −2.31 ± 0.32‰ for non-N$_2$-fixing trees). This pattern likely reflects the use of the same N sources by the species of both functional groups at the subhumid site. Contrary to what occurs at the subhumid site, leaf δ^{15}N and enrichment factors varied between functional groups at the semiarid site ($\Delta\delta^{15}$N leaf – soil: -3.03 ± 0.29‰ and -1.81 ± 0.30‰ for potential N_2-fixing and non-N_2-fixing trees, respectively), which suggests that a portion of N used by N_2-fixing trees could derive from atmospheric N_2. Thus, our data indicate a flexibility in N acquisition in the legumes species studied, which may employ a facultative strategy of utilizing N from fixation only in cases of transient N limitation of ecosystem processes (see Hedin *et al.* 2009, Barron *et al.* 2011, Soper *et al.* 2015), as has been suggested previously for the semiarid site (Campo 2016).

CONCLUSIONS

The future of tropical forests is uncertain; particularly, the regulation of major biogeochemical cycles is expected to be modified by changes in climate conditions, especially changes in precipitation regime (Barbosa & Asner 2017). Our results indicate that a decrease in annual precipitation potentially will lead to the deregulation of internal N cycling, possibly exacerbating losses of the nutrient from the ecosystem through gas loss. In a scenario in which decreases in mean annual precipitation could lead to greater N losses as N_2O, the ecological implications could be a negative feedback loop, whereby changes in climate lead to lower rainfall amounts, greater greenhouse gas emissions as N_2O, a further change in climate since tropical forests are a major regulator of global climate. We found a more open N cycle in the drier site with a high prevalence for N loss, compared to a more closed N cycle in the wetter site, similar to past studies (Craine *et al.* 2015b) We cannot determine whether these patterns in N cycling resulted from the decrease in primary productivity and decomposition with greater drought intensity, or whether the more open N cycle in the drier site reflects the increase in legume abundance under semiarid climate, or both. These possible direct and indirect effects of rainfall on the biogeochemistry of TDFs highlight the need for new efforts to understand the impact of changes in climate on the ecology of tropical dry forests.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vr24515 (Rivero-villar *et al.* 2018).

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Capítulo III

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Nitrogen cycling in tropical dry forests is sensitive to changes in rainfall regime and nitrogen deposition

Anaitzi Rivero- Villar, Gerardo Ruiz- Suárez, Pamela H. Templer, Valeria Souza,
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Resumen

El impacto de los cambios en los regímenes de lluvias y la deposición de nitrógeno (N) atmosférico en los ciclos biogeoquímicos de los bosques tropicales secos (BTS) siguen sin estar claros. Para analizar si las cantidades de precipitación anual media (1240 mm año^{-1} en bosques subhúmedos vs 642 mm año^{-1} en bosques semiáridos) y las tasas de deposición de N atmosférico afectan el ciclo del N en BTS, examinamos las concentraciones de N en (i) hojas verdes , (ii) suelo forestal y capas de suelo mineral, y (iii) biomasa microbiana del suelo, así como (iv) abundancia natural de δ^{15}N en hojas verdes y (v) tasas de actividad enzimática del suelo y (vi) pérdidas de N en dos sitios (uno subhúmedo y otro semiárido) de Yucatán. El sitio semiárido tuvo concentraciones más altas de N en las hojas y en ambas capas del suelo que su contraparte subhúmeda. La abundancia natural δ^{15}N en la vegetación sugiere un ciclo de N más abierto conforme disminuye la lluvia, lo que fue corroborado por las pérdidas de N como óxido nitroso (N_2O) que son dos veces más altas en el sitio semiárido en comparación con el subhúmedo. Un ciclo de N más abierto sujeto a mayores pérdidas en respuesta a la adición de N en el sitio semiárido, pero no en el sitio subhúmedo, refuerza que las cantidades de lluvia afectan fuertemente el ciclo de N en BTS.

Palabras clave: Sequía, ENSO, pérdidas de N, emisiones de N_2O, abundancia natural ^{15}N

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Nitrogen cycling in tropical dry forests is sensitive to changes in rainfall regime and nitrogen deposition

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Abstract The impacts of changes in rainfall regimes and atmospheric nitrogen (N) deposition on the biogeochemical cycles of tropical dry forests (TDF) remain unclear. To analyze whether amounts of mean annual rainfall (1240 mm year^{-1} in subhumid vs. 642 mm year^{-1} in semiarid forests) and rates of atmospheric N deposition affect the N cycle in TDF, we examined N concentrations in (i) green leaves, (ii) forest floor and mineral soil layers, and (iii) soil microbial biomass, as well as (iv) $\delta^{15}N$ natural abundance in green leaves and (v) rates of soil enzyme activity and (vi) N losses in two sites (one subhumid and another semiarid) of Yucatan. The semiarid site had higher N concentrations in leaves and both soil layers than its subhumid counterpart. Natural abundance $\delta^{15}N$ in the vegetation suggests a more open N cycle with lower rates of rainfall, which was corroborated by N losses as nitrous oxide (N_2O) being twice as high in the semiarid compared to subhumid site. A more open N cycle subject to greater losses in response to N addition in the semiarid site, but not in the subhumid site, reinforce that rainfall amounts strongly affect N cycling in TDF.

Keywords Drought · ENSO · N losses · N_2O emissions · ^{15}N natural abundance · Mexico

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Introduction

Climate models estimate substantial changes in rainfall regimes across tropical regions throughout the twenty-first century (IPPC 2013; Knapp et al. 2015). Variation in rainfall amount will increase and likely lead to prolonged and intense periods of droughts, affecting tropical regions such as tropical dry forests (TDF), which historically experience alternating rainy and dry seasons (Miles et al. 2006; Chadwick et al. 2016). Droughts will affect TDF function locally (Campo and Merino 2016; Allen et al. 2017) and will also influence global biogeochemical cycles since TDF cover approximately 42% of tropical land globally (Murphy and Lugo 1986). The tropical forest biome is a major hotspot of the global nitrogen (N) cycle as these ecosystems are responsible for 70% of global terrestrial N fixation and 62% of global nitrous oxide (N_2O) emissions (Hedin et al. 2009;

Townsend et al. 2011; Bai et al. 2012; Tian et al. 2018) in terrestrial land covered by native vegetation.

Nitrogen is an essential element that regulates ecosystem dynamics and functions, including primary productivity (Chapin et al. 1986; Güsewell 2004; Elser et al. 2007; Vitousek et al. 2010); changes in N inputs could have large effects on both nutrient cycling within forest ecosystems and the balance of nutrient fluxes into and out of tropical forest lands (Elser 2011; Bejarano-Castillo et al. 2015; Craine et al. 2018). Atmospheric N inputs have increased globally by a factor of 10 since pre-industrial times (Galloway et al. 2008; Gruber and Galloway 2008) with large changes observed in tropical regions (Tian et al. 2019) as a consequence of high rates of N fertilizer applications in agroecosystems (Rockstöm et al. 2009; Steffen et al. 2015). For the coming decades, rates of atmospheric N deposition in tropical forests are expected to be similar to or exceed the rates of biological fixation, and some models expect a fourfold increase in atmospheric N inputs in comparison to current amounts (Dentener et al. 2006; Sullivan et al. 2014). However, our ability to understand the effects of this increase in N inputs on ecosystem N cycles is challenged by the heterogeneity of the tropical forest biome from a local to regional scale, in response to the broad combination of abiotic (soil age and chemistry) and biotic (high diversity in plant species) conditions (Townsend et al. 2008).

Increases in atmospheric N deposition could result in greater N retention or saturation, enhancing N losses by leaching and/or denitrification (Aber et al. 1989; de Vries and Schulte-Uebbing 2019). In a meta-analysis examining impacts of experimental N addition in tropical forests, Bejarano-Castillo et al. (2015) reported multiple responses to N addition, but the magnitude and direction of the responses was sensitive to the initial N status of the forest ecosystems. In sites limited by N, some of the added N was immobilized by forest vegetation, which resulted in lower rates of N losses by leaching. In contrast, in tropical forest ecosystems not limited by this element, N additions increased rates of N losses via leaching. In general, N_2O emissions increased regardless of the initial N status. Globally, N_2O emissions from soils have increased from 6.3 Tg year^{-1} in the preindustrial period to 10 Tg year^{-1} today as a consequence of diverse anthropogenic factors such as atmospheric N deposition (Tian et al. 2018). Tropical soils remain the primary source of N_2O emissions, accounting for $\sim$ 53% of new global emissions (Tian et al. 2018). However, the impacts of changing climate, such as the projected increase in drought frequency and intensity (Chadwick et al. 2016), on the ability of tropical forests to retain or lose excess N is unknown. Thus, further research is necessary to understand the response to elevated rates of atmospheric N deposition in the context of changing rainfall regimes in N-rich regions such as tropical forest biomes (Lee et al. 2019).

Previous studies in TDFs of Yucatan, Mexico show that differences in rainfall regimes influence rates and patterns of N cycling. Both N concentration and $\delta^{15}N$ natural abundance in vegetation and soils are higher as rainfall decreases, regardless of the tree species (i.e. potential N_2-fixing or non- N_2-fixing plants), demonstrating that the difference in N cycling between these sites can be attributed mainly to local rainfall conditions and not plant functional groups (Rivero-Villar et al. 2018). The patterns of $\delta^{15}N$ in vegetation and soil of these forests indicate that a decrease in mean annual rainfall leads to a more open N cycle (Roa-Fuentes et al. 2015; Rivero-Villar et al. 2018). A lower amount of annual rainfall leads to a more open N cycle as a consequence of the uncoupling between plant N uptake and soil microbial N transformations, leading to greater N losses from the ecosystem (Reichmann et al. 2013; Wang et al. 2014).

Nitrogen fertilization experiments in TDFs of Yucatan suggest the N cycling responses to increased atmospheric N inputs are likely to vary depending on rainfall. Results from a microcosm experiment showed there to be lower soil microbial biomass carbon (C) and N, but increased losses of CO_2 and N_2O, at the semiarid compared to subhumid site (Bejarano et al. 2014a). Although there is experimental evidence that net primary production increases in response to increased N inputs to TDF ecosystems (Campo and Vázquez-Yanes 2004), information is lacking on the functional response to the combined effects of changes in the rainfall regime and N deposition under field conditions. This lack of data limits our understanding of how these global environmental changes will affect tropical dry forests in the future.

Our objectives were (i) to determine the effects of mean annual rainfall on N cycling in TDFs and (ii) to evaluate the impact of increased rates of N deposition on N dynamics in two TDFs in Yucatan. We answered the question: How does mean annual rainfall (MAR) and atmospheric N deposition combine to affect internal N cycling and ecosystem N losses? To answer this question, we carried out field experiments in two TDF sites receiving different amounts of MAR (1240 mm year^{-1} in a subhumid vs. 642 mm year^{-1} in a semiarid site) in Yucatan. The experiment at both sites included a systematic N addition rate of 24 kg N^{-1} ha^{-1} year^{-1} over the last decade. Potential differences in N cycling due to altitude, air temperature, parent material, and vegetation type were excluded by keeping these factors consistent across the two sites. We measured (i) N concentration and ^{15}N natural abundance in green leaves, (ii) N concentration in the organic and mineral soil layers, (iii) N concentration in soil microbial biomass, and (iv) rates of N losses from the ecosystems via N leaching and N_2O emissions.

Considering previous studies of the N cycle in TDFs of Yucatan (Roa-Fuentes et al. 2015; Campo and Merino 2016; Rivero-Villar et al. 2018), we expected three possible outcomes: (i) if rainfall is the main driver of the N cycle in these ecosystems, we expected to observe decreasing N concentrations in vegetation and soil as rainfall decreases, as a result of greater N losses; in this case N_2O emissions would be the main pathway of N losses from these ecosystems; (ii) if N additions are the main driver of the N cycle, we expected to observe an increase in N concentration in vegetation and soils, which would lead to increased loss of N from the ecosystem as both leachate and N_2O, regardless of the rainfall regime; and (iii) if together, rainfall and N addition are both the main drivers of N cycle, we expected N additions would result in increased N retention by both vegetation and soil microbial biomass at the semiarid site, since these TDFs may be N-limited and therefore we expected very low rates of N loss, whereas we expected increases in N losses in the subhumid site since it may not be N-limited.

Material and methods

Study region and experimental design

The study was carried out in two mature TDFs with contrasting rainfall regimes (one semiarid and the other subhumid) in Yucatan (Figs. 1 and 2). The drier semiarid site is located in the north of Yucatan and receives approximately half the mean annual rainfall of the wetter subhumid southern site (Table 1). Long-term climate data from Mexico's National Weather Service shows that both sites are characterized by a distinct period of low rainfall during the dry season, which corresponds to 5 to 7 months with rainfall below 100 mm per month (Fig. 2; Table 1). Variation in mean annual temperature between both sites is less than 1 °C, and the climate, semiarid to subhumid, supports both tropical very dry or dry forests in the Holdridge life zone system (Holdridge et al. 1971).

The landscape of both sites is relatively flat with < 50 m of altitudinal variation between study sites (Table 1). The predominant lithology in both sites includes late Pliocene material, with large areas of exposed limestone. Soils in the Yucatan Peninsula are derived from Tertiary limestone in a typical karstic landscape of flat rock outcrops and shallow depressions (Bautista et al. 2011), and generally fall into two groups: shallow black soils (*Lithic usthortens*) surrounding rock outcrops, and deeper red soils (*Lithic haplustolls*) at slightly lower relief. Soils in the semiarid site are mainly black soils (*Lithic usthortens*); with increased MAR increases red soils (*Lithic haplustolls*) in the cover area, which are the dominant soils at the subhumid site. At the semiarid site, the pH of the soils is higher (8.1 ± 0.05; mean ± 1 SE) and soils are less dense due to the greater amount of soil organic matter compared to the subhumid site (pH at subhumid site = 7.6 ± 0.07; Campo and Merino 2016; Table 1). Soil water retention is greater at the wetter site, with soils having 33% field capacity at the semiarid site and 66% field capacity at the subhumid site (Roa-Fuentes et al. 2012), reflecting differences in soil clay content (31.7 ± 6.1% and 56.1 ± 1.5% at the semiarid and subhumid sites, respectively). The native vegetation in both sites is the TDF. Dominant tree species across all sites are *Bursera simaruba* (L.) Sarg. (*Burseraceae*), *Gymnopodium floribundum* Rolfe (*Polygonaceae*), and two potential N_2-fixing associated species, *Piscidia piscipula* (L.) Sarg. and *Lysiloma latisiliquum* (L.) Benth (Roa-Fuentes et al. 2015).

These forest sites are part of an N addition experiment established in 2007. The aim of this long-term experiment is to simulate the highest rates of N deposition expected for the tropical region by the year 2030 (32 kg N ha^{-1} year^{-1}; Dentener et al.

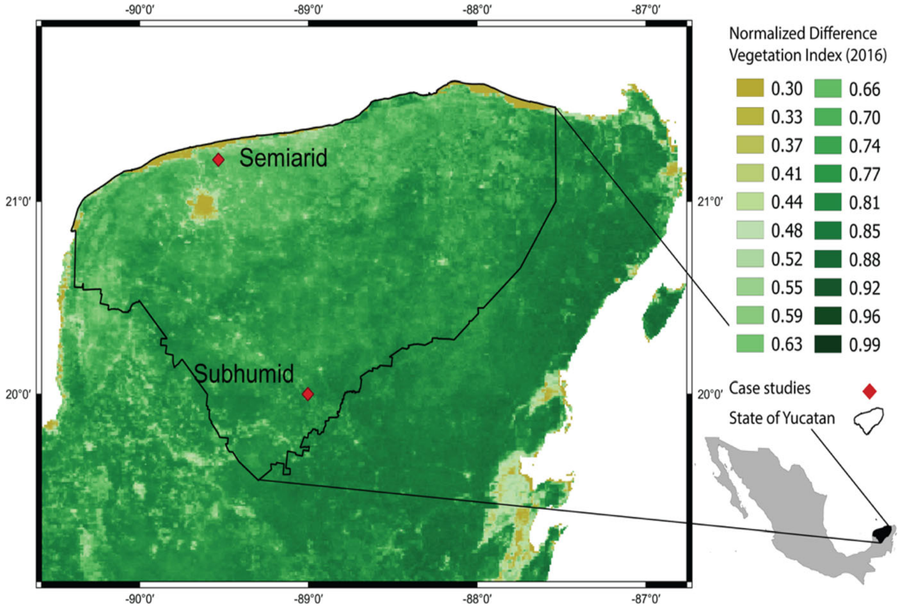


Fig. 1 Map of field study sites in the Yucatan Peninsula, Mexico. Green colors indicate Normalized Difference Vegetation Index (NDVI) in the study year (2016; A. Rivero-Villar unpublished data)

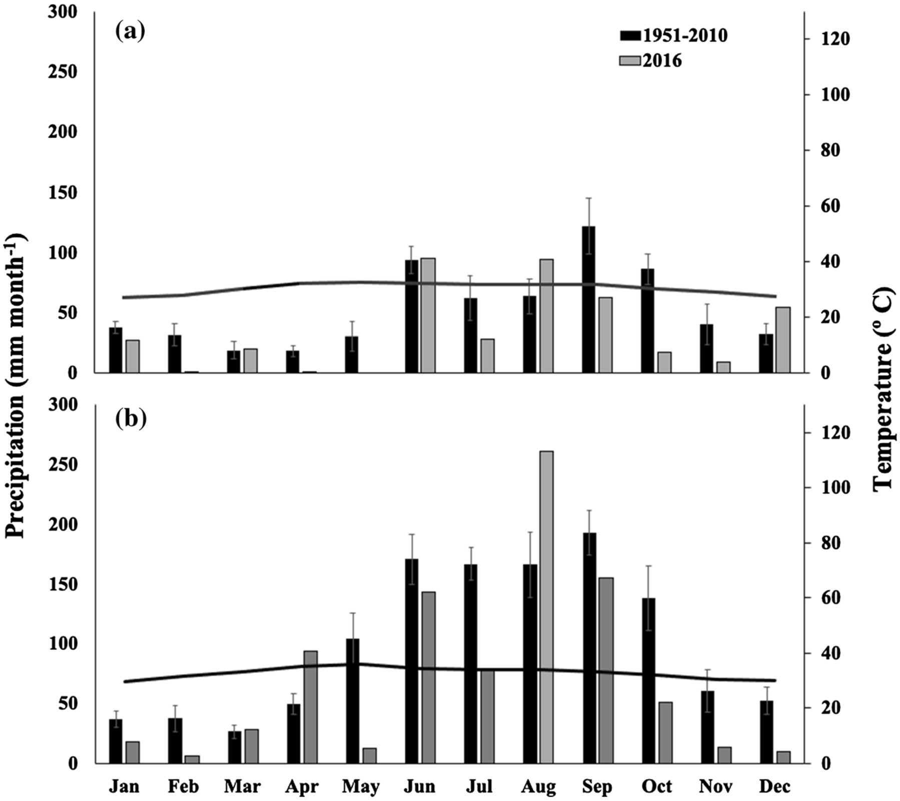


Fig. 2 Monthly rainfall (bars) and temperature (solid line) in semiarid (**a**) and subhumid (**b**) sites in the Yucatan Peninsula, Mexico. Long-term climatic data (1951–2010) in black bars and study year climatic data (2016) in gray bar (Mexican National Weather Service- CONAGUA)

Table 1 General characteristics of the study sites

	Semiarid site	Subhumid site
Coordinates	21° 13′ N, 89° 32′ W	20° 48′ N, 89° 26′ W
Altitude (m)	3 ± 3	36 ± 9
Climate[b]	Warm semiarid	Warm subhumid
	BS1	Aw1
Mean annual temperature (°C)[a]	25.8 ± 2.5	25.5 ± 2.1
Mean annual rainfall (mm year^{-1})[a]	642 ± 43	1240 ± 89
Evapotranspiration potential ratio (mm mm^{-1})[a]	2.67	1.39
Dry season months[a]	November–May	December–April
Mineral soil (0–10 cm)[b]		
Bulk density (g m^{-3})	0.70 ± 0.06	0.91 ± 0.05
Soil clay content (%)	31.7 ± 6.1	56.1 ± 1.5
Field capacity (%)	33.1	65.6
Vegetation[c]		
Tree height (m)	3.03 ± 0.22	5.35 ± 0.19
Basal area (m^2 ha^{-1})	30.1 ± 5.2	30.9 ± 4.9
Tree density (stem ha^{-1})	2598 ± 338	3923 ± 441
Aboveground biomass (Mg ha^{-1})	47.4 ± 7.23	65.6 ± 9.70
Belowground biomass (Mg ha^{-1})	22.1 ± 1.15	19.3 ± 0.17

[a] Mexican National Weather Service- CONAGUA (years 1950–2014)

[b] García (2004)

[c] Roa-Fuentes et al. (2012)

2006). At the beginning of the experiment, eight plots (each 12 × 12 m) were established at each site with an 8 m buffer between each plot. Four plots receive ambient levels of atmospheric N deposition (control plots; approximately 8 kg N ha^{-1} year^{-1}), and the remaining plots receive the equivalent of 24 kg N ha^{-1} year^{-1} plus ambient atmospheric N deposition (+ N plots) amounting to a total of 32 kg N ha^{-1} year^{-1}, which is similar to the rate of atmospheric N deposition expected by 2030. Nitrogen is added at the end of each dry season (May) with polymer-coated controlled-release urea (Multicote fertilizer [8] 40-00-00, Haifa Chemical), which typically releases its N content over 4 to 6 months. In this study, we report the responses to 10 years of N addition from samples collected in 2016. The year of our study was the warmest to date over the last 137 year-period, due to the influence of a strong El Niño- Southern Oscillation (ENSO) event (NOAA 2017). In Mexico, the year 2016 was particularly warm and dry (CONAGUA 2017a). Both study sites were affected by this abnormally dry condition with a reduction of 37 and 30% in the annual rainfall amount that received the semiarid and subhumid sites, respectively (CONAGUA 2017b).

Sample collection

To determine the effects of N addition and changes in rainfall regime on N cycling, green leaves of each tree and soil samples from the organic and top mineral (0–10 cm in depth) soil layers were collected in each plot of both sites in September 2016. Samples were collected in the middle of the rainy season, since this is when most plant N uptake and soil microbial processes leading to N transformations occur in these forests.

Eighty mature trees per treatment (diameter at the breast height, dbh ≥ 5 cm) (n = 20 trees per plot × 4 plots) were randomly chosen at each site. To understand the effect of N additions on these TDFs, we focused on vegetation as whole, not on the role or effect of specific tree species; thus, we did not identify the trees species. However, all were deciduous tree species and were similar across sites (Roa-Fuentes et al. 2015). By sampling extensively across tree species in similar function groups (all deciduous trees), we aimed to understand the response of N cycling in TDFs broadly, rather than to focus on specific tree species.

Green leaf samples were collected to determine foliar concentrations of N as a proxy for the N status in vegetation supported by the evidence that N allocation is conserved across plant organs in woody plants (Heineman et al. 2016; Zhao et al. 2016). We measured natural abundance ^{15}N values in foliage to determine the relative openness of the N cycle in each plot and site. We sampled only mature and healthy leaves (without visible signs of herbivory or disease), randomly selecting and collecting full sunlit branches from all parts of the canopy. Foliage was sampled by a telescopic tree branch cutter. The leaves were kept in paper bags and air-dried to prevent rotting.

Within each plot, five polyvinylchloride (PVC) rings (20 cm in diameter), which contained only dead plant material, including fresh fallen litter and the more finely decomposed litter fraction, were randomly selected. Forest floor litter (henceforth forest floor) and a sample of the mineral topsoil (0–10 cm in depth) were collected from each ring. The samples of each soil layer were combined to obtain one composite sample for the forest floor layer and one for the mineral topsoil layer per plot. All forest floor layer and mineral topsoil layer samples were stored at 4 °C until processing.

Samples of N leachate from below the upper 10 cm depth of the soil profile and N_2O emitted from soils in each plot were analyzed at the same time to determine rates of N loss from each plot and site. At two randomly selected spots in each plot we installed one lysimeter suction cup (1900 Soil Water Sampler, Soilmoisture®). During the installation we tried to cause as little disturbance to the soil as possible: the holes were hand-drilled, the depth of each lysimeter was 10 cm or at lithic contact. The collection of leached water samples started 36 h after the lysimeters installation, allowing the soil to stabilize. A single sample per lysimeter was collected daily during the next five days after the stabilization period. Four rain events occurred in each site (rainfall amount per day from the first to fifth days was 1, 0, 9.9, 1.5 and 12.5 mm day^{-1} in the semiarid site, and 22, 0, 1, 3 and 7 mm day^{-1} in the subhumid site) during the sampling period. The two soil water samples were combined per day and per plot. By the end of the fifth day of sampling we obtained 28 samples per site (14 from the N addition plots and 14 from the control plots), as during the days of the experiment not all lysimeters contained water. To prevent contamination of the samples we supplied an aliquot ($\sim$ 1 μL) of ethanol-free chloroform and stored lysimeter samples at 4 °C until analysis.

We placed a static chamber for field gas flux measurements near each lysimeter. The static chambers were composed of two parts: (i) a 17 cm diameter and 20 cm tall PVC ring and (ii) a PVC internal cap with a single injection port (rubber septum). Rings were inserted 5 cm into the soil, with 15 cm between the soil surface and the chamber lid. As with the lysimeters, the gas samples were taken 36 h after installation and collected at the first, third, and fifth days following installation. In each sampling date three gas samples were taken at 0, 30, and 60 min after the chambers were closed, using a needle (double ending); the longer part of the needle was inserted in the injection port and the shorter inside of a pre-evacuated glass container. The three samples per chamber (i.e. at 0, 30, and 60 min) were used to estimate the N_2O flux (μg N_2O cm^{-2} h^{-1}) in each sampling date.

Analytical methods

The leaves, forest floor, and mineral soil were oven-dried at 60 °C for 48 h. The petiole of leaves was removed previous to chemical and isotopic analysis. Forest floor and mineral soil samples were homogenized, and root material in the mineral soil samples were removed prior to sieving using a 2 mm mesh. The leaves were ground in an agate mortar to obtain a homogenized fine powder.

Nitrogen concentration and δ^{15}N natural abundance in green leaves were measured in the Stable Isotope Laboratory of Boston University. Leaf samples were combusted in a Euro EA elemental analyzer and the combustion gases were separated into a gas chromatography column, passed through a GV Instruments diluter and reference gas box, and analyzed for ^{15}N abundance using a GVI IsoPrime isotope ratio mass spectrometer.

We report all stable isotope data as natural abundance δ^{15}N values, representing the ratio between each foliar sample and that of atmospheric dinitrogen using the following equation:

$$\delta^{15}\mathrm{N} = \left\{\left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1)\right\} \times 1000$$

where R_{sample} represents the sample isotope ratio (^{15} N/^{14} N) and R_{standard} is ^{15} N/^{14} N for atmospheric N_2 (0.0036765).

Total N concentration in forest floor samples was determined from acid digestion in concentrated H_2SO_4 for Kjeldajl N (Anderson and Ingram 1993) and analyzed using an NP element analyzer (Technicon Autoanalyzer). The pH of mineral soil layer was analyzed in deionized water. The total N concentration in mineral soil was determined from acid digestion in H_2SO_4 concentrated for Kjeldajl N (Anderson and Ingram 1993) and analyzed using an NP element analyzer (Technicon Autoanalyzer). Inorganic N (NH_4^+ and NO_3^-) concentrations were determined by extraction from fresh soil sub-samples with 50 mL of 2 M KCl, shaken for 60 min, and allowed to settle and filtered through a Whatman No. 1 paper filter (Robertson et al. 1999). A 20 mL aliquot supernatant was transferred to sample vials and frozen for later analysis. The analysis was performed with an autoanalyzer system using procedures for NO_3^--N plus NO_2^--N determination, reported as NO_3^--N, and the salicylate–hypochlorite procedure for NH_4^+–N.

Microbial biomass N (MBN) concentration in mineral soil was determined using chloroform fumigation-extraction (Brookes et al. 1985; Vance et al. 1987) with replicated samples of fresh mineral soil. Fumigated and non-fumigated samples were incubated for 24 h at 24 °C. Microbial biomass N was extracted from both fumigated and non-fumigated samples using 0.5 M K_2SO_4 and Whatman No. 42 paper filter; the filtrate was digested in acid and the total concentration of N in both (i.e. fumigated and non-fumigated) soil samples was determined using an NP element analyzer. Concentrations of N in the non-fumigated extracts were subtracted from concentrations in the fumigated extracts, and microbial N was estimated using a conversion factor (k_N) for microbial N equal to 0.57 (Jenkinson 1987). Urease activity was measured using urea as the substrate, and the NH_3 released in the hydrolysis reaction was analyzed (Nannipieri et al. 1980).

Soil leachate samples were vacuum-filtered through a membrane (Millipore 0.45 μm HV), and the inorganic N concentrations (i.e. NO_3^- and NH_4^+) were determined by colorimetry (Technicon Autoanalyzer). Gas samples were stored at room temperature and analyzed on a gas chromatograph (Shimadzu GC-2014) equipped with an electron capture detector, ECD, 325 °C, for N_2O and an autosampler with a sample loop injector (1 mL,120 °C). N_2 was used as a carrier gas (flux 25 mL min^{-1}). Gas concentrations were determined by comparison with a calibration curve and its integrated peak areas. Calibration curve points were determined using certified standard, and the N_2O flux was estimated using the values for the 0, 30 and 60 min per chamber.

Statistical analysis

For each variable, a two-way ANOVA was performed to test differences between sites (semiarid vs subhumid) and treatments (control vs N-addition) and their potential interaction. The residuals were explored for normality and variance homogeneity using the Shapiro–Wilk's test and Levene's test, respectively. Data were transformed logarithmically when the assumptions of normality and homoscedasticity did not occur. For the δ^{15}N natural abundance in green leaves, transformed data did not fulfill the assumptions of normality and homoscedasticity, and therefore a nonparametric test was used (Kruskal–Wallis test). For soil solution water samples and soil N_2O fluxes, we built a linear model. For the soil leachate samples, the model was formulated to test for potential differences between sites, N treatments, days of sampling, amount of leached N and the interactions among all these factors. For the N_2O flux linear model, we included as variables, site, N treatments, day of sampling, and soil temperature. For all analyses, a significance level of $p < 0.05$ was used. The honest significant difference (HSD) test was used when statistical differences ($p < 0.05$) were observed. All the statistical analyses were performed using R software (R Development Core Team 2016).

Results

Nitrogen in vegetation

Nitrogen concentration and δ^{15}N natural abundance in green leaves from the control plots of the semiarid site were higher than those from the subhumid site ($F = 53.82$, $p < 0.001$, for the N concentration; $\chi^2 = 174.22$, $p < 0.001$, for $\delta^{15}N$ natural abundance) (Fig. 3). The $\delta^{15}N$ in green leaves range from 0.51 to 9.89‰ in the control plots of the semiarid site and from − 0.81 to 6.57‰ in the control plots of the wetter site. Nitrogen addition increased significantly the N concentration in green leaves at the semiarid site ($F = 10.84$, $p = 0.001$) (Fig. 3a). However, the natural abundance of $\delta^{15}N$ in leaves was insensitive to N additions ($\chi^2 = 0.108$, $p = 0.742$) (Fig. 3b). The green leaves in N addition plots of the semiarid site had a wider $\delta^{15}N$ range compared to those of the fertilized plots in the subhumid site (by a factor of around 8 in the case of the semiarid site, from 1.32 to 10.02‰, and by a factor greater than 5 in the case of the subhumid site, from − 0.01 to 5.48‰).

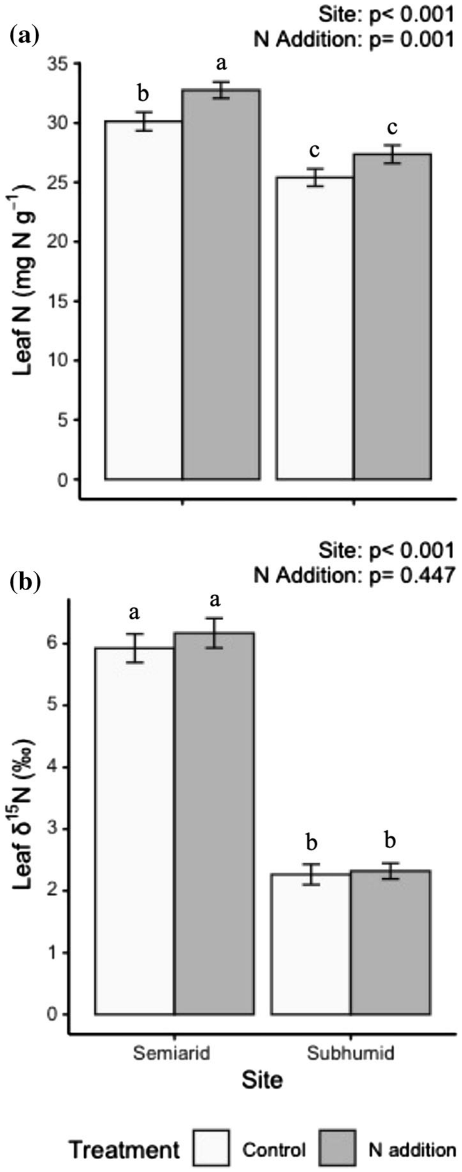


Fig. 3 Nitrogen concentration (**a**) and $\delta^{15}N$ natural abundance (**b**) in leaves under two treatments of nitrogen addition in a semiarid and a subhumid site of the Yucatan Peninsula. Values are means ± 1 SE (n = 80 per treatment)

Nitrogen in forest floor and mineral topsoil

Nitrogen concentrations in the forest floor were higher in the control plots of the semiarid site than in the subhumid site ($F = 16.32$, $p = 0.004$; Fig. 4a); however, N concentrations in the forest floor were not significantly affected by N addition ($F = 0.45$, $p = 0.507$). Total N (Fig. 4b) and inorganic N concentrations (Fig. 5a, b), and the NO_3-N:NH_4-N ratio (Fig. 5c) in the mineral topsoil were also greater in the drier site ($F = 36.46$ to 203.79, $p < 0.001$). Total N and NO_3^--N concentrations in the mineral topsoil increased with N addition in the semiarid site ($F = 14.93$, $p = 0.001$, for total N; $F = 6.02$, $p = 0.020$, for the NO_3^--N; Figs. 4b, 5b), and increased in a marginally significant manner for the NH_4^+-N concentration ($F = 4.00$, $p = 0.053$; Fig. 5a). The NO_3^--N:NH_4^+-N ratio did not vary with N addition (Fig. 5c).

Microbial biomass N in soils of the control plots of the semiarid site were greater than soils of the subhumid site; $F = 4.98$, $p = 0.033$; Fig. 6). The microbial N contribution to total N in the mineral soil (measured as the ratio between the N in microbial biomass and total N in topsoil) ranged from 2.3 to 7.9% including all observation from both sites. A greater proportion of the total soil N was bound up in microbial biomass in the subhumid site than in the semiarid site (6.0 ± 0.5% and 3.8 ± 0.3%, respectively; $F = 13.06$, $p = 0.001$). Neither MBN concentration nor the microbial N contribution to total N in the mineral topsoil (4.1 ± 0. 7% and 5.2 ± 0.4% for the semiarid and subhumid site, respectively) changed in response to N addition ($F = 1.42$, $p = 0.242$, for the MBN concentration; and $F = 0.31$, $p = 0.581$ for the MBN: total N ratio; Fig. 6). Urease enzyme activity was significantly higher in the control plots of the semiarid site than in the subhumid site ($F = 21.87$, $p < 0.001$), and increased significantly in response to

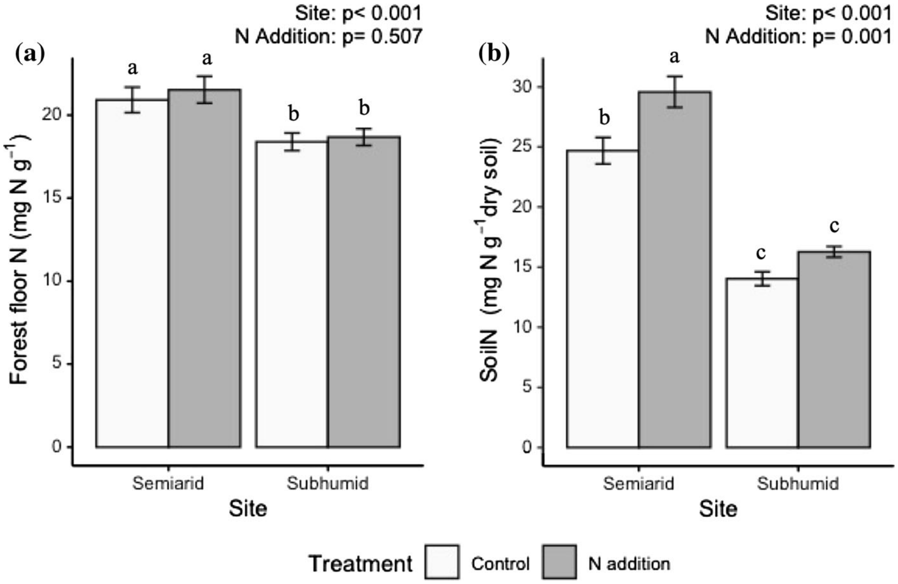


Fig. 4 Nitrogen concentration in forest floor (**a**) and topsoil (**b**) under two treatments of nitrogen addition in a semiarid and a subhumid site of the Yucatan Peninsula. Values are means ± 1 SE (n = 8)

the N enrichment in the subhumid site ($F = 7.13$, $p = 0.012$) (Table 2).

Nitrogen losses from the ecosystem

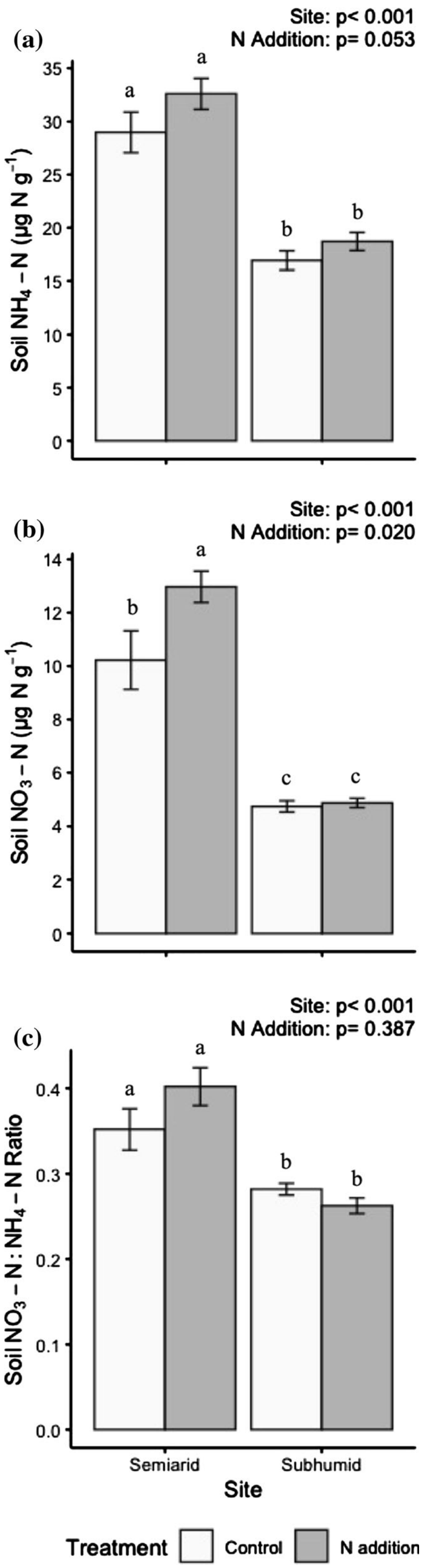
The accumulated volume of leached water recovered per site after 5 days was approximately six times greater in the subhumid site than in the semiarid site (155 ± 13 mL and 26 ± 1 mL, respectively), showing the effects of the differences in rainfall amount on soil water between study sites ($\chi^2 = 41.32$, $p < 0.001$). As in the control plots, the volume of soil solution water was ~ 6 times lower in the semiarid site (25 ± 1 mL) relative to the subhumid site (141 ± 20 mL) in the N addition plots.

At both sites the concentration of NO_3^- -N in soil solution was greater than that of NH_4^+-N- (by ~ 164 times in the semiarid site and by ~ 80 times in the subhumid site) (Fig. 7a, b). The NO_3^--N concentration in leached water was greater in the drier site ($F = 65.23$, $p < 0.001$), meanwhile those for NH_4^+-N did not vary between sites ($F = 3.21$, $p = 0.079$). The amount of inorganic N leached (estimated as the product of the nutrient concentration by the water volume recovered) was lower in the semiarid site than in the subhumid site ($\chi^2 = 25.80$, $p < 0.001$ for the NO_3^--N; and $F = 53.37$, $p < 0.001$, for the NH_4^+-N) (Fig. 7c, d), reflecting differences in water volume. The N addition increased significantly both inorganic N leachate concentrations in the semiarid site ($F = 5.89$, $p = 0.019$ for the NO_3^--N; $F = 7.15$, $p = 0.010$, for the NH_4^+-N; Fig. 7a, b). However, only the total mass of NH_4^+-N in soil solution estimated as the product of its concentration by the water volume was significantly higher in the N fertilized plots than in control plots at the semiarid site ($F = 4.18$, $p = 0.045$) (Fig. 7c). In contrast, the mass of NO_3^- -N in soil solution was not affected by N fertilizer additions ($p > 0.05$).

Nitrous oxide fluxes were not significantly different between sites ($p > 0.05$; Table 3). However, the proportion of µg N_2O h^{-1} losses relative to the NO_3^--N content in the mineral soil considering the depth, density, and stoniness of the soil layer at each site (data not showed), were higher in semiarid site than in the subhumid counterpart ($F = 53.25$, $p < 0.001$) (Fig. 8). In contrast, the N addition did not affect N_2O fluxes from soils, even considering these losses relative to the NO_3^--N content in the mineral topsoil (Table 3 and Fig. 8).

Discussion

This study provides a quantitative overview of the effects of both rainfall regime and atmospheric N inputs on the N cycle of two TDFs in southeastern Mexico. Our results demonstrate the great sensitivity of N cycling dynamics in these ecosystems to the expected increase in the frequency and intensity of the



◀**Fig. 5** Ammonium (**a**) and nitrate (**b**) concentrations, and nitrate:ammonium ratio (**c**) in topsoil under two treatments of soil nitrogen addition in a semiarid and a subhumid site of the Yucatan Peninsula. Values are means ± 1 SE (n = 8)

extreme climatic events such as droughts in this region, as well as the expected increase in atmospheric N deposition over time. These changes in rainfall regime and N deposition are likely to induce further opening of the N cycle, ultimately leading to greater N losses as rainfall decreases and N inputs from atmospheric N deposition accumulate over time.

Effects of rainfall on the N cycle of tropical dry forests

We found greater N concentrations in foliage, microbial biomass, forest floor, and topsoil in the site with lower mean annual rainfall, reflecting greater soil N availability in the mineral layer of the soil and a change in plant traits with a greater leaf N in trees at the semiarid compared to subhumid site, probably to compensate for the expected high photosynthetic rates induced by reduced stomatal conductance under water-stress (Santiago et al. 2017). Similar to past observations across a larger and wetter rainfall gradient (1800 to 3500 mm year^{-1}) in tropical lowland forests, the foliar nutrient concentration decreases in response to the increase in water availability (Santiago et al. 2005). We conclude that the observed changes in foliar N concentration are related to plant response to rainfall regimen and not to plant community composition since we sampled from a large diversity of plant species that were all deciduous trees, discard major changes in to plant composition between our study sites (see Roa-Fuentes et al. 2015) or differences in N economy and requirement of the dominant species (i.e. N$_2$-fixing or non-N$_2$-fixing plants; Rivero-Villar et al. 2018). The greater accumulation of N in soils at the drier site may be related to lower rates of organic matter decomposition (Bejarano et al. 2014b; Powers et al. 2015) due to lower water content in soils limiting microbial activity that drives decomposition and soil N transformations (Levy-Booth et al. 2014; Pajares et al. 2018; Chen et al. 2019; Tatsumi et al. 2019).

The higher δ^{15}N values in foliage of the semiarid site in comparison to the wetter site suggests a more open N cycle in TDFs with lower rates of rainfall.

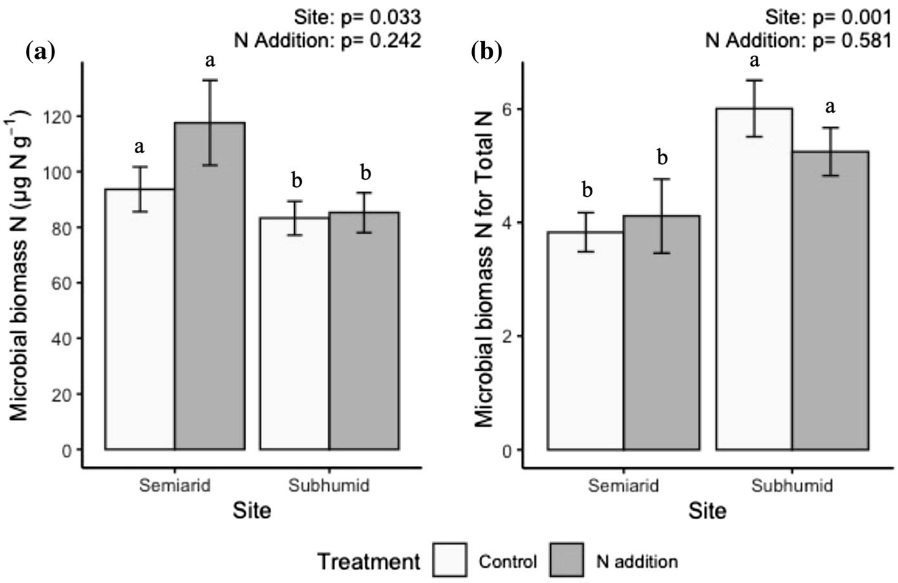


Fig. 6 Microbial biomass nitrogen concentration (**a**) and microbial biomass nitrogen contribution to total nitrogen (**b**) in topsoil under two treatments of soil nitrogen addition in a semiarid and a subhumid site of the Yucatan Peninsula. Values are means ± 1 SE (n = 8)

Table 2 Urease enzyme activity in topsoil under two treatments of nitrogen addition in a semiarid and a subhumid sites of the Yucatan Peninsula

	Semiarid		Subhumid	
	Control	+ N	Control	+ N
Urease enzyme activity (µmol NH_4^+-N g^{-1} h^{-1})	10.5 ± 0.5^a	11.2 ± 0.8^a	5.2 ± 0.5^c	9.2 ± 1.4^b

Distinct letters represent statistically significant differences among site and treatment. Values for each site are means ± SE (n = 8)

Consistent with a global meta-analysis (Craine et al. 2009) and with previous observations at the same TDFs in the Yucatan Peninsula of Mexico (Roa-Fuentes et al. 2015; Rivero-Villar et al. 2018), $\delta^{15}N$ signatures in vegetation (leaves and roots) and soils are higher in sites with less rainfall, regardless of tree species, however only at the semiarid site the leaf $\delta^{15}N$ signatures varied among potential N_2- fixing and non-N_2- fixing trees, suggesting a facultative strategy in N acquisition in the legumes species in case of N limitation (Rivero-Villar et al. 2018). Nevertheless, we found a $\delta^{15}N$ foliar enrichment at both site in comparation to Rivero-Villar et al.'s study, this may suggest that N fixation at this season was constrained by the water limitations, since N fixation cost is elevated, and it is only cost effective under sufficiently severe N limitation (Menge et al. 2017). We therefore attribute the higher $\delta^{15}N$ values in foliage to the $\delta^{15}N$ enriched soils at the semiarid site due the opening of the N cycle and not to differences among plant functional groups. These results demonstrate that as climate change leads to a greater frequency of extreme weather events such as droughts, the N cycle in TDF ecosystems is likely to open further. And the particular adaptation of the species to N acquisition may not be enough to respond to the new conditions.

Fluctuations of wet and dry years in the future could exacerbate the asynchrony between soil N availability and plant N acquisition in dry years, making these TDF ecosystems prone to N losses when dry years are followed by wet years (Reichmann et al. 2013). Water pulses after a rainless period could stimulate biological N transformations, enhancing NO_3^- leaching and N_2O emissions, as has been observed in other tropical ecosystems where the magnitude of N gas emissions are related to the length and intensity of the previous

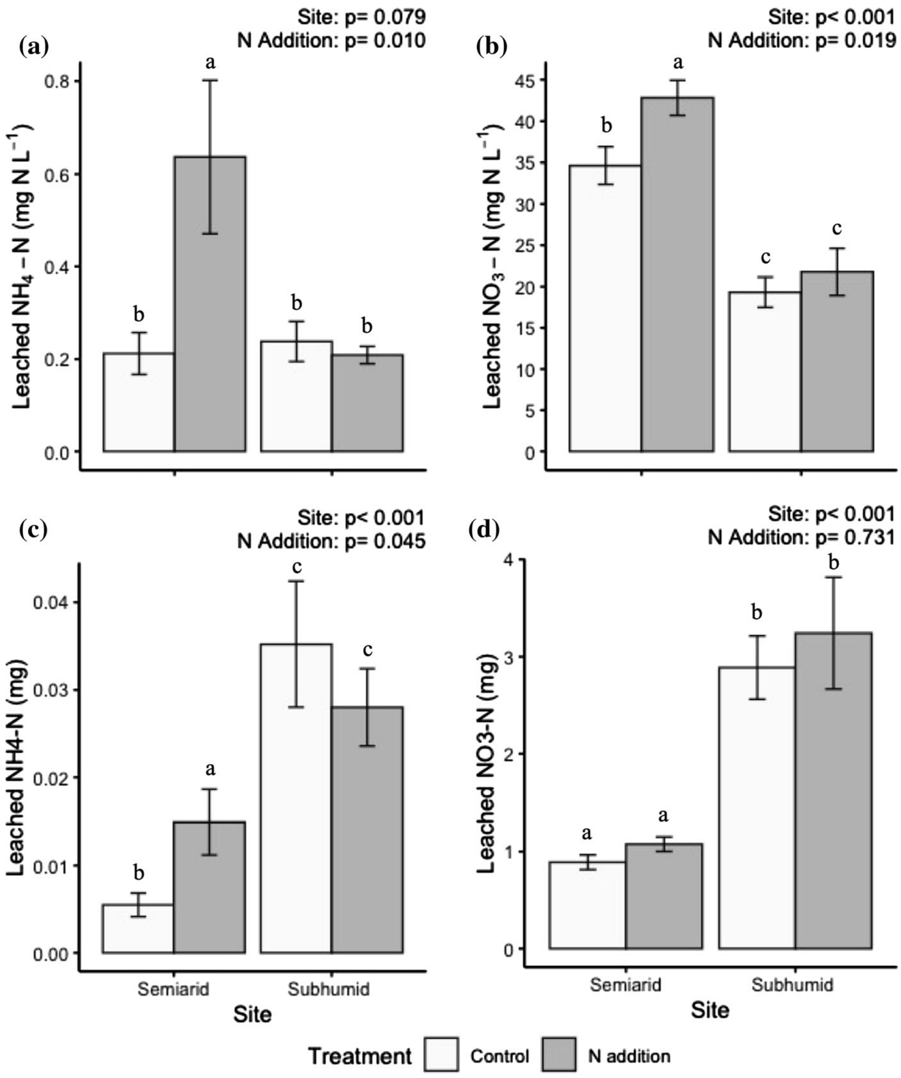


Fig. 7 Ammonium (**a**) and nitrate (**b**) concentrations; ammonium (**c**) and nitrate (**d**) mass, in leaching water under two treatments of soil nitrogen addition in a semiarid and a subhumid site of the Yucatan Peninsula. Values are means ± 1 SE (n = 14)

dry period (Read et al. 2019; Welch et al. 2019; Calvo-Rodriguez et al. 2020). Moreover, the greater N concentrations in the leached water observed at our semiarid site suggest that the rainfall events leads to greater nutrient leaching as aridity conditions increase.

According to Luévano-Arroyo (2018) experimental evidence using a ^{15} N tracer indicates that 75% of N inputs to the soil are retained in the soil–plant system of Yucatec TDFs, and the contribution of leaching to N loss is greater than that by denitrification (24% by leaching and 1% by N_2O emissions), in concordance with our findings. Our results show that the NO_3^- leaching from the TDF soils is greater at the drier site, reflecting the large NO_3^- concentration in mineral soils. Also, the proportion of N lost as N_2O from soils at the semiarid site was almost double the amount of N emissions at the subhumid site. The availability of suitable substrate (e.g., NO_3^-) is more important than whether soils are waterlogged or well drained in determining the emission levels of greenhouse gases like N_2O (Vitousek et al. 1989; Welch et al. 2019).

Our results show significant variation in N cycling between forest sites, supporting the argument that arid ecosystems are less efficient in regulating the N cycle than wetter ecosystems (Craine et al. 2015b; Roa-Fuentes et al. 2015; Soper et al. 2015; Rivero-Villar

Table 3 Nitrous oxide fluxes under two treatments of nitrogen addition in a semiarid and a subhumid site of the Yucatan Peninsula

	Semiarid site		Subhumid site	
	Control	+ N	Control	+ N
N_2O flux (μg N_2O cm^{-2} h^{-1})				
Day 1	3.13 ± 0.39	3.41 ± 0.47	4.96 ± 0.51	4.50 ± 0.70
Day 3	3.87 ± 0.56	4.85 ± 0.64	3.47 ± 0.86	3.37 ± 0.62
Day 5	4.23 ± 0.87	4.9 3 ± 0.86	3.24 ± 0.55	3.34 ± 0.69
Mean	3.74 ± 0.36^a	4.40 ± 0.40^a	3.56 ± 0.37^a	3.73 ± 0.39^a
N_2O flux (μg N_2O cm^{-2} h^{-1}/μg NO_3^- g $soil^{-1}$)				
Day 1	4.41 ± 0.79	3.8 2 ± 0.53	2.81 ± 0.58	2.42 ± 0.37
Day 3	5.01 ± 0.57	5.45 ± 0.75	2.18 ± 0.55	1.28 ± 0.36
Day 5	5.91 ± 1.02	5.85 ± 0.83	2.54 ± 0.73	1.71 ± 0.37
Mean	5.11 ± 0.47^a	5.05 ± 0.46^a	2.51 ± 0.35^b	1.98 ± 0.21^b

Distinct letters represent statistically significant differences among site and treatment. Values for each site are means ± SE (n = 24)

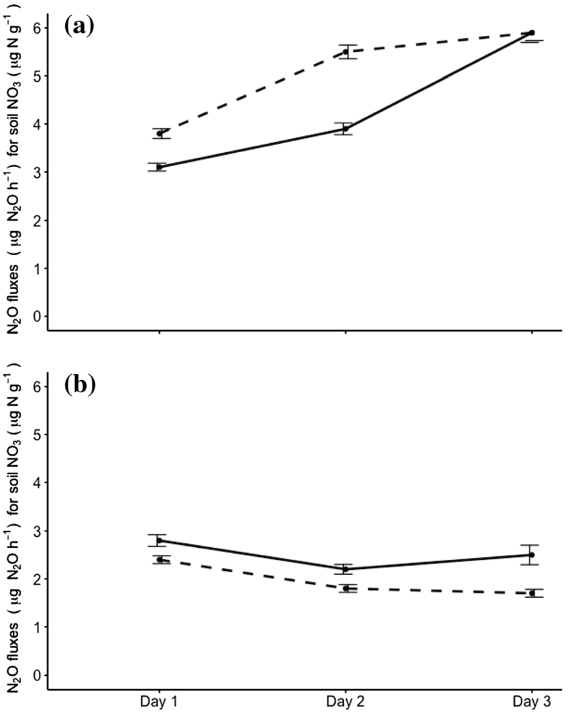


Fig. 8 Nitrogen oxide fluxes under two treatments of soil nitrogen addition (control (continuous line) and nitrogen enrichment (dashed line) plots) in a semiarid (**a**) and a subhumid forests site (**b**) of the Yucatan Peninsula. Values are means ± 1 SE (n = 24)

et al. 2018). The relatively low amount of rainfall for 2016, the year of our study was a strong El Niño year, and likely caused a $\delta^{15}N$ foliar enrichment of approximately 18 and 10% at the semiarid and subhumid sites, respectively, compared to the same experimental plots measured in a typical rainy season such as 2014 when the annual rainfall was similar to the long-term historic average (Rivero-Villar et al. 2018); showing that the large N losses reported here were likely driven by microbial transformations, since soil microbes strongly discriminate against the heavy isotope (Houlton and Bai 2009; Craine et al. 2018). Also, in comparison to the mean values of Rivero-Villar et al. (2018), total soil N decreased ~ 13 and 37% at the semiarid and subhumid sites, respectively, suggesting that drought opens the N cycle in TDF ecosystems, in accordance with Craine et al. (2015a) who found that rainfall regimes exert a long-term control over the N cycle in terrestrial ecosystems.

The N_2O emissions in TDFs are lower than in other tropical forests (Castaldi et al. 2006; Calvo-Rodriguez et al. 2020). In our study the N_2O fluxes were lower than those reported for humid tropical forests (Vitousek et al. 1989; Corre et al. 2010), but comparable to those reported for other TDFs (0.32 to 12.9 mg N_2O m^{-2} day^{-1}; Castaldi et al. 2006), including others in Mexico (Vitousek et al. 1989; García-Méndez et al. 1991; Davidson et al. 1993; Bejarano et al. 2014a). We attribute the low levels of N_2O emissions in our study to the low rainfall amount in the sampling period (50 and 20% lower rainfall than the long-term average for the semiarid and subhumid sites, respectively; Fig. 2) since other studies have demonstrated that rainfall amount is a key driving factor of N_2O emissions

(Butterbach-Bahl et al. 2004; Konda et al. 2010; Calvo-Rodriguez et al. 2020). The small amount of annual rainfall during the year of our study likely reduced water infiltration in TDF soils, and thus limited soil N transformations (Chen et al. 2019) similar as shown at other Mexican TDF, were low rainfall (10 mm) did not stimulate soil P availability (Campo et al. 1998). In addition, soil drying in the very low rainfall year of 2016 could have reduced the availability of dissolved organic carbon, with potential negative effects on nitrification and denitrification (Chen et al. 2019).

We found difference in daily N_2O emissions across the two sites, since changes in water availability affects rates of nitrification and denitrification, which contribute to N_2O emissions (Butterbach-Bahl et al. 2004; Rowlings et al. 2012). There was a slight increase after rain events at the semiarid site; the N_2O fluxes after the biggest rain event (12 mm) increased in comparison to other sampling dates (from 4.4 to 5.9 µg N_2O h^{-1} by soil NO_3^--N µg) in the semiarid site. In contrast, in the subhumid site, the difference between the wettest and driest days did not have significant differences in N_2O emissions (2.2 to 2.8 µg N_2O h^{-1} by soil NO_3^--N concentration) even when the amount of rainfall was almost double (22 mm). Drought conditions were more severe at the semiarid site; the incoming rain may have sharply reactivated N_2O emissions, as occurs in other TDFs (Vitousek et al. 1989, 1997; García-Méndez et al. 1991; Corre et al. 2010; Bejarano et al. 2014a). Moreover, increases in the magnitude of the N_2O pulses associated with rewetting events has been observed during El Niño years in tropical forest ecosystems (Zhang et al. 2019; Calvo-Rodriguez et al. 2020). In other Mexican TDFs, large rainfall events ($\geq$ 10 mm) were positively correlated with litter decomposition rates (Anaya et al. 2012), indicating that the amounts of rain in TDFs are enough to activate microbial activity and gaseous N emissions from soils.

Effects of N additions on the N cycle of tropical dry forests

Our results reflect the biogeochemical effects of systematic N addition to TDF ecosystems over a 10-year period. Some tropical forests are sensitive to the amount and duration of N addition (Bejarano-Castillo et al. 2015). Our study provides evidence that vegetation (leaf N concentration), topsoil (total N and NO_3^- concentrations), soil N-acquisition enzyme (urease activity), and N losses from TDFs via soil leaching increase in response to elevated rates of N addition, irrespective of the rainfall regime. Moreover, the TDFs of the semiarid site have a more open N cycle relative to those of the subhumid site and are more sensitive to the expected increase in atmospheric N deposition, exacerbating the opening of the N cycle in these ecosystems.

There are multiple pathways through which forest ecosystems may respond to anthropogenic N deposition. Time and magnitude of responses depend on the initial N status of each forest (Aber et al. 1989). A meta-analysis conducted by Bejarano-Castillo et al. (2015) indicates that tropical forests' responses to N addition is related to the forest N status. Increases in N inputs favors N uptake by TDF trees (Campo and Dirzo 2003; Campo et al. 2007; Mao et al. 2020). As we expected, some of the additional N from our fertilizer inputs was retained by the vegetation (foliar N concentration increased ~ 6 and 8% in N addition plots) at both semiarid and subhumid forest sites; however, only for the semiarid site the difference in leaf N concentration between N treatments was statistically significant, suggesting that vegetation in this drier site is N-limited, probably related to an openness of the N cycle. Recent experimental evidence in the Costa Rican TDFs indicates that nutrient availability and primary productivity in these forests were contingent on both water availability and functional plant diversity, although in general plants seem to be more restricted by drought stress than nutrient availability (Waring et al. 2019). We agree that water availability is a strong driver of the forest response to nutrient addition and may even co-limit net primary productivity in these water-limited ecosystems. We understand that plants display multiple strategies to responses to new nutrient availability according to its intrinsic stoichiometric requirements, depending on plant functional groups. However, a long-term nutrient addition experiment in a tropical montane forest demonstrates that most plant species respond (increasing tree growth, higher leaf N and P concentration and higher specific leaf area) to increases of N (and also P) soil availability, regardless of the particular acquisitive functional traits, since the plant community has the potential to modulate the effects of increased nutrient deposition (Báez and Homeier 2018), prior to N saturation.

Stable isotopic discrimination during N uptake is strongly related to balance between plant demand and soil supply. When N supply changes in response to N addition, a drop down in the $\delta^{15}N$ of foliage (Choi et al. 2003; Fuentes-Mendizábal et al. 2018) can be expected, since plants discriminate in favor of the lighter isotope (Sheng et al. 2019). However, the foliar $\delta^{15}N$ values in our N-addition plots were not significantly different from the foliar $\delta^{15}N$ in the control plots. We cannot determine whether such a lack of foliar $\delta^{15}N$ response to N addition reflects that vegetation is using all the soil N available irrespective of it being the light or heavy isotope in response to a potential N limitation or because the variability in specific N demand in TDF trees (Campo and Dirzo 2003), or both. Although we did not measure the $\delta^{15}N$ content of the N fertilizer we applied, literature values indicate that $d^{15}N$ abundance of synthetic fertilizers are typically close to 0‰ since they reflect the $\delta^{15}N$ signature of the atmosphere, which by convention is zero (Choi et al. 2003; Bateman and Kelly 2007; Craine et al. 2015b). Rather than reflecting the isotopic values of fertilizer itself, we conclude that foliar $\delta^{15}N$ values are more likely to reflect soil N that resulted from microbial processes that plants took up.

A previous study conducted in the same experimental plots did not find differences in total soil N concentration after four years of N addition (Bejarano et al. 2014a). However, our data show that the mineral topsoil layer in TDFs has increases in the total N (of 3 and 2% for the semiarid and subhumid sites, respectively) and the inorganic NO_3^- (NO_3^- concentration increased by 21% in the semiarid site and by ~ 3% for the subhumid site) accumulation after 10 years of chronic N-addition, despite the fact that N losses from the ecosystem increased over this period. In contrast, the NH_4^+ concentration in the mineral soil did not increase after N chronic addition, likely due to greater uptake of NH_4^+ than NO_3^- by vegetation in TDFs (Luévano-Arroyo 2018). Our results also indicate that soil microbial biomass was not sensitive to the fertilizer N inputs, as shown in moist tropical forests (Templer et al. 2008). Thus, although we did not find an increase in soil N immobilization by microbial biomass in response to the N additions, our study provides evidence of N retention by vegetation, as well as total N and inorganic (NO_3^-) N accumulation in the soil that could be lost by leaching and denitrification.

Contrary to our prediction, our results indicate an increase in N losses from the forest ecosystem via leaching, with a larger change observed at the semiarid than subhumid site. Even though the fraction of NH_4^+ leached in comparison to NO_3^- is small, a large increase in NH_4^+ leached observed in the semiarid site is important since it is the form of inorganic N plants in these ecosystems take up more of (Luévano-Arroyo 2018). This increase in NH_4^+ losses in the semiarid site may suggest that the vegetation is less efficient in uptake of soil available N due low water conditions, or even that as the forest productivity drops (Campo and Merino 2016) the nutrient demand decrease, or both, leading to a greater uncoupling between soil nutrient availability and its vegetation uptake in response to drought increase. As has been observed in a Costa Rican TDF, where a sever ENSO drought reduced primary productivity by up to 40% (Castro et al. 2018). On the other hand, the observed increase in NO_3^- leaching from the TDF in response to the experimental N addition suggests that the expected increase in atmospheric N deposition could be a future environmental concern in Yucatan due to the potential negative effects of NO_3^- leaching on nearby “cenotes”, aquatic ecosystems.

Surprisingly, N_2O emissions were not affected significantly by our N additions. Nitrogen oxides emissions are more related to nutrient limitation than to the length of ecosystem exposure to N addition; e.g., more N_2O and NO gases were observed in P-limited forests than in N-limited forests, despite amounts and years of N addition (Corre et al. 2010; Bejarano-Castillo et al. 2015; Müller et al. 2015; Tang et al. 2018). Our previous work indicated that N_2O emissions increase in response to N enrichment under controlled laboratory conditions with soils collected from the semiarid site (Bejarano et al. 2014a). We attribute the difference between our results and the previous observation by Bejarano et al. (2014a) mainly to differences in rainfall regimes in each study period. Bejarano et al.’s study was performed in a year with total rainfall amount close to the long-term MAR, in 2010, in contrast to the drier year of our study, 2016. We are aware that the evidences from this study does not demonstrate an N_2O emissions increases in responses to the N addition, however, if the N addition slightly stimulates N_2O losses at the semiarid site as apparently occurs, coupled to the previous evidence shown by Bejarano et al.'s, and our evidence of more NO_3^- leaching at semiarid site, together supports our idea that changes in rainfall regime and N deposition are likely to induce further opening of the N at the driest condition.

Conclusions

Our study contributes to the understanding of how the N cycle in tropical dry forests responds to global environmental changes expected in the near future, including the intensification of drought and the increase in atmospheric N deposition. Our results demonstrate that elevated rates of atmospheric N inputs will have local impacts that could produce a global negative feedback to climate change, as the increase in N_2O emissions from the drier site with elevated N demonstrate that emissions of this greenhouse gas may increase in the future. Our findings reinforce the evidence that the N cycle in these forests is strongly affected by rainfall regimes, with increased N inputs leading to greater plant N uptake, soil N availability, ecosystem openness, and N losses, especially in drier sites. Together, these results show that tropical dry forest ecosystem responses to the increase in N inputs from the atmosphere could be exacerbated by the expected decrease in rainfall amount over the coming decades. Given the crucial role of tropical forests in global carbon and nitrogen cycles, the findings of the present study warrant further research on the potential negative feedbacks of these changes on global climate change.

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Data availability Data supporting the findings of this study are available upon request.

Declarations

Conflict of interest None of the authors have any conflict of interest to declare.

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Discusión general y conclusiones

El estudio de la dinámica de los ciclos biogeoquímicos a través de distintos enfoques y uso de diversas herramientas, nos permitirá tener entendimiento más amplio del funcionamiento de los ecosistemas terrestres, y su respuesta ante los cambios globales. Los resultados de esta investigación reafirman la importancia que desempeña la disponibilidad de agua en este tipo de ecosistemas, la cual tiende a ser el factor preponderante en la modulación y dinámica de los ciclos biogeoquímicos (Jaramillo & Sanford, 1995; Powers et al., 2018; Campo & Merino, 2019) tanto a escala local como regional. Si bien la estructura y función de los bosques tropicales se encuentran fuertemente controlado por las condiciones edáficas y climáticas, para los bosques tropicales secos la variación en el régimen de lluvias es el factor más determinante, como lo pudimos observar tanto en los patrones globales de lC, N y P del suelo (*Capítulo I*); así como localmente en la dinámica del ciclo del N de los bosques tropicales secos de Yucatán (*Capítulo II y III*)).

Conclusiones de los objetivos 1 y 2*: "Los suelos de los paisajes de bosques tropicales secos son dominantemente de baja fertilidad; La gran heterogeneidad biogeoquímica, se encuentra fuertemente determinada por la variabilidad climática, particularmente por la cantidad de precipitación anual que reciben; Las variables relacionadas con la fertilidad del suelo demostraron ser altamente sensibles a las variaciones en la aridez"*

La revisión pantropical corrobora la gran heterogeneidad biogeoquímica de los suelos en los bosques secos (Townsend et al. 2011; Waring et al., 2021). Los resultados, sugieren que los almacenes de C, N y P responden a diferentes impulsores ambientales, particularmente están estrechamente acoplados a las variaciones locales del régimen de lluvias. Como se ha observado en otros bosques BTS, la duración de la estación húmeda puede en parte determinar el almacenamiento de C orgánico del suelo, a mayor humedad habrá mayor C orgánico en el suelo (Rohr et al., 2013). La menor disponibilidad de agua se ha asociado a bajas tasas de descomposición de la materia orgánica (Bejarano et al. 2014, Campo & Merino 2016), que, tiende a modificar la tasa de reciclaje de nutrientes a la comunidad microbiana del suelo y la vegetación (Campo, 2016). En general los indicadores de fertilidad considerados en este trabajo demostraron ser vulnerables a la disponibilidad de agua y al incremento en la aridez. Las regiones de menor precipitación demostraron tener los suelos con los menores contendidos de C orgánico, N y P totales, así como una menor capacidad de intercambio catiónico, que puede ser reflejo de la baja productividad y de la calidad de materia que se está reincorporando a estos suelos. En el caso del C orgánico, se podría deber a un menor almacenamiento, reforzando así las observaciones de Rohr y colaboradores (2013).

El cambio climático es una de las muchas presiones que experimentan las regiones tropicales secas, acorde a los modelos de cambios climáticos proyectados para mediados de este siglo, bajo escenarios de cambio severo la región podría experimentar un incremento de 2.5ºC o la disminución en la precipitación media anual en 50 mm al año (Miles et al., 2006). En este sentido, se espera que el cambio climático desacoplará los ciclos biogeoquímicos, en particular, se espera que la regulación de ciclos biogeoquímicos se vea modificada por cambios especialmente en el régimen de precipitaciones (Barbosa & Asner 2017). El poder predecir la magnitud y trayectoria de estos cambios y su retroalimentación con el cambio climático global, representa uno de los mayores desafíos que enfrenta la ecología de ecosistemas secos (IPCC, 2021). Esta vulnerabilidad puede tener consecuencias graves más allá de las ecológicas, pudiendo poner en riesgo la seguridad alimentaria, los medios de vida y el bienestar de las personas que habitan en la región: cerca del 25% de la población mundial vive y depende de los BTS (Djoudi et al., 2015; Sunderland et al., 2015; Schröder et al., 2021).

A escala de ecosistema se tiene poca información unificada, que permita hacer inferencias más finas, por ello los resultados de este primer capítulo son de gran relevancia, ya que representa el primer esfuerzo de síntesis que conjuga características edáficas, biogeoquímicas y climáticas. Sin embargo, aún falta tener mayores evidencias que sustenten que la tendencia de los BTS ante el incremento en la aridez está directamente relacionada con la disminución de los almacenes de nutrientes del suelo como lo siguieren nuestros resultados, además de que haría falta trazar el destino de los nutrientes y su retroalimentación con la biogeoquímica y el cambio climático a escala local y global. Por lo que en los *Capítulos II y III* a través un estudio de caso, buscamos dilucidar qué le ocurrirá al ciclo del N particularmente ante los escenarios de cambio global como ya se ha reiterado lo largo de esta investigación.

Conclusiones de los objetivos 3 y 4: *"El ciclo interno de N de los bosques de Yucatán se encuentra fuertemente modulado por el régimen de lluvias, el sitio más seco tiene una alta prevalencia a la pérdida de N, es decir tiene un ciclo de N más abierto que el subhúmedo; El incremento esperado de N afecta su ciclo interno, sin embargo, el efecto de la adición se encuentra modulado por el régimen de lluvias, exacerbando las pérdidas de N conforme disminuye el régimen de lluvias, generando ciclos más abiertos que tendrán una retroalimentación positiva al cambio climático global; Los eventos climáticos atípicos tienen un fuerte impacto en la dinámica del ciclo del N, ocasionando el* *desacoplamiento temporal del nutriente en el sistema planta-suelo, ocasionando una mayor apertura de los ciclos tras períodos de sequía"*

Mediante el uso de isótopos estables (*Capítulos II y III*) pudimos corroborar que el clima es un importante impulsor del ciclo de N de los bosques secos de Yucatán, lo cual es consistente con estudios previos en la región (Campo & Vázquez-Yanes, 2004; Roa-Fuentes, 2015; Bejarano, 2014 a; Campo, 2016; Campo & Merino, 2016) y con las tendencias globales, las cuales muestran que la abundancia natural de ^{15}N varía sistemáticamente a lo largo de gradientes climáticos (Amundson et al., 2003; Craine et al., 2015). El δ^{15}N enriquecidos del suelo y la vegetación en el sitio semiárido reafirman que la aridez conduce a una mayor apertura del ciclo del N en estos bosques en comparación con la contraparte más húmeda, lo cual podría ser una señal de que a mayor disponibilidad de agua mayor eficiencia en el ciclaje del N a través de los diferentes compartimentos del ecosistema (Soper et al., 2015). La hipótesis de una mayor apertura en el ciclo conforme aumenta el déficit hídrico fue corroborada a través del estudio de los flujos y salidas de N del sistema, sin embargo, en contraposición a lo que esperábamos la principal vía de pérdida se dio aparentemente por lixiviación, como también fue reportado por Luévano-Arroyo (2018).

A su vez, los resultados se suscriben a las tendencias observadas en otros BTS, que demuestran cambios en la dinámica de los ciclos biogeoquímicos como consecuencia del cambio climático, principalmente en respuesta a cambios en el régimen de precipitación o a un evento extremo (i.e. El Niño) (Sánchez-Azofeifa et al., 2013; Castro et al., 2018; Calvo-Rodriguez et al., 2020, 2021). De llegar a condiciones severas de aridez en la región de Yucatán, como se ha proyectado en los escenarios de cambio climático para la Península (Orellana et al., 2009), esperaríamos que el ciclo del N fuese menos conservativo. Como consecuencia sería más agudo el desacople temporal entre la disponibilidad de N y la demanda biológica, lo que podría llevar a una menor productividad de estos bosques, generando una acumulación de nutrientes en el suelo, susceptible de perderse ya sea en forma gaseosa y/o lixiviada.

Por otro lado, pudimos corroborar mediante el experimento de adición de N que el incremento de los depósitos de N atmosféricos está exacerbando la apertura de su ciclo, sin embargo, los efectos de la adición se encuentran fuertemente modulados por el régimen de lluvias y el ciclo interno de cada sitio, por lo cual observamos una menor regulación del ciclo en el bosque semiárido similar a lo reportado por (Bejarano et al., 2014). Esto se vio reflejado en el incremento de las pérdidas de N en dicho sitio. Si bien parte del N adicionado aún está siendo retenido por la vegetación, esperaríamos que, de mantenerse la productividad de estos bosques bajo condiciones crónicas de depósitos de N, el ciclo se abriría aún más, tanto en el sito semiárido como en el subhúmedo, repercutiendo en el calentamiento global.

Los resultados sugieren que la lixiviación es un importante mecanismo de pérdida de N en estos bosques. Lo cual representa una gran preocupación dada las características de los suelos y la litología de la península. La Península de Yucatán presenta un sistema hidrológico único, que se caracteriza por la ausencia de corrientes superficiales, con frecuentes y voluminosos acuíferos subterráneos, que forman un sistema de vasos comunicantes que desembocan en el mar. La zona vadosa está compuesta por calizas fracturadas, lo que permite que el agua se infiltre rápidamente al acuífero, llevando todo tipo de compuestos orgánicos disueltos y otros contaminantes (Velázquez-Aguirre, 1986, Herrera-Silveira et al.2004). Por lo tanto, la pérdida de N a los cuerpos acuáticos está generando problemas de eutrofización que es una de las mayores preocupaciones en la Península de Yucatán, particularmente para el sitio semiárido, dada su proximidad a la zona costera. Las consecuencias ecológicas de las grandes pérdidas hidrológicas de N no se conocen bien, sin embargo, el acuífero se considera vulnerable a la contaminación superficial (Canul-Macario et al. 2019).

Perspectivas

Si bien los resultados indican que los cambios globales están modificando la dinámica del ciclo del N a escala regional, estas evidencias siguen sin ser suficientes para predecir los cambios a escala del bioma. Por ello, resulta prioritario aumentar el monitoreo a múltiples escalas y de largo plazo, así como realizar experimentos que controlen la disponibilidad de agua y las tasas de aumento de N, en la mayor cantidad de BTS del mundo. Este esfuerzo deberá contemplar una visión más holística que integre desde la comunidad microbiana del suelo, hasta los patrones de productividad y los procesos de descomposición de la materia orgánica. En general, estos monitoreos deberán explorar los efectos antagónicos o sinérgicos que ocurren al modificar los patrones naturales, incluyendo los efectos sobre otros bioelementos clave, ya que es esperable que cambios en los flujos de N tenderán a modificar la relación estequiométrica con el C y el P, y en general, las dinámicas ecológicas de la región.

Además, resulta prioritario incluir en los estudios no solo el efecto de los cambios globales ya mencionados sino de ser posible contemplar otros factores de cambio que también están influyendo en la dinámica biogeoquímica de estos bosques; por ejemplo, el aumento de la incidencia de incendios, o el proceso de sucesión secundaria. Particularmente se debe de poner mayor énfasis en la investigación de los bosques secundarios, ya que estos son el tipo de bosque dominante, históricamente han sido menos estudiados que los bosque maduros, en parte debido a que la investigación tradicional se centra en ecosistemas no perturbados (Powers & Marín-Spiotta, 2017; Estrada-Villegas et al., 2020). Comprender los patrones de sucesión y los mecanismos que los subyacen es fundamental porque los procesos ecosistémicos y los ciclos biogeoquímicos responden a y actúan como impulsores del cambio en las comunidades bióticas durante la sucesión.

En general tener una visión más integral de los cambios que enfrentan los BTS nos permitirá tener una mayor certeza para inferir el punto de inflexión del sistema y establecer así mejores políticas de conservación y manejo con fines de mitigación y adaptación a estos cambios, en particular para mejorar las proyecciones del cambio climático.

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