Check for updates

Received: 13 June 2023 | Revised: 10 January 2024 | Accepted: 2 February 2024

DOI: 10.1002/ece3.11037

RESEARCH ARTICLE

Ecology and Evolution Open Access WILEY

Environment predicts *Batrachochytrium dendrobatidis* lineage distribution and zones of recombination in South Africa

Ruhan Verster[1] | Pria N. Ghosh[1,2] | Tom R. Sewell[2] | Trenton W. J. Garner[1,3] | Matthew C. Fisher[2] | Wynand Muller[1] | Dirk Cilliers[1] | Ché Weldon[1]

[1]Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa

[2]MRC Centre for Global Infectious Disease Analysis, School of Public Health, Imperial College London, London, UK

[3]Institute of Zoology, Zoological Society of London, London, UK

Correspondence
Ruhan Verster, Unit for Environmental Sciences and Management, North-West University, South Africa.
Email: ruhan.verster@gmail.com

Funding information
Centre for Ecology and Hydrology, Grant/Award Number: MRC MR/R015600/1, NE/K012509/1, NE/S000992/1 and NERC NE/S000844/1

Abstract

The amphibian-infecting chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*), is widespread throughout Africa and is linked to declines of populations and species across the continent. While it is well established that the lineage of *Bd* encodes traits which determine disease severity, knowledge around how lineages are distributed according to environmental envelope is unclear. We here studied the distribution of *Bd* in South Africa based on the two lineages found, *Bd*GPL and *Bd*CAPE, in terms of their genome and environmental envelope statistically associated with their distribution. We used *Bd* surveillance data from published studies, as well as data collected during fieldwork from across South Africa, Lesotho, and eSwatini with samples collected along a transect spanning most of South Africa from Lesotho to the west coast. We utilized lineage-typing qPCR to resolve the spatial distribution of *Bd*GPL and *Bd*CAPE across South Africa and used the resulting surveillance data to create a predictive ecological niche model for *Bd* lineages in South Africa. Phylogenomic analyses were performed on isolates sourced from across the transect. We show that *Bd*GPL demonstrates a strong isolation by distance suggestive of stepping-stone dispersal, while *Bd*CAPE showed two distinct clusters within their genomic structure that appear geographically and temporally clustered, indicating two separate invasions. Our predictive niche model revealed that the two lineages tended to occur in different ecotypes; *Bd*GPL was associated with lower altitude, arid regions while *Bd*CAPE occurred across cooler, higher altitude environs. Niche predictions identified a zone of lineage contact, where genomics identified inter-lineage recombinants. We argue that this zone of recombination should be prioritized for disease surveillance as it is a potential hotspot for the evolution of variants of amphibian chytrid with novel traits that may be epidemiologically relevant.

KEYWORDS
Africa, amphibian chytrid fungus, distribution modeling, environmental envelope, predictive ecological niche modeling, recombinant zone

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

TAXONOMY CLASSIFICATION
Biodiversity ecology, Conservation ecology, Disease ecology, Zoology

1 | INTRODUCTION

Across our globalized planet, pathogens are frequently translocated, sparking epidemics that threaten human, livestock, crop, and wildlife health. Pathogens, once established, go on to adapt to naïve hosts through the processes of mutation, lineage sorting, and recombination—processes that can lead to a changing epidemiological landscape. Global-scale pandemics are characterized by successive waves of emergence as genetically distinct lineages spread. However, while better understood for viruses such as SARS-CoV-2 (Harvey et al., 2021), we have poor understanding of the extent that the epidemiology of fungal pathogens owes to lineage-specific traits that characterize emerging lineages. We have even less understanding of the evolutionary changes that occur in pathogens when recombination generates novel genotypes. These evolutionary "jumps" have the potential to lead to phenotypic changes of large consequence leading to lineage replacement by newer, fitter variants that may propagate spatiotemporal waves of infection (Fisher et al., 2012)

Batrachochytrium dendrobatidis, (*Bd*), and *B. salamandrivorans* are two pathogenic chytrid fungi that have emerged to infect amphibians around the globe (Martel et al., 2013). The disease that they cause, chytridiomycosis, has contributed to the decline of over 500 amphibian species and is believed to be responsible for the extinction of over 90 species (Scheele et al., 2019). The epidemiology of chytridiomycosis is complicated by the fact that *Bd* to date is known to comprise of at least five lineages, with observed differences in infectivity and virulence when tested (Byrne et al., 2019; Farrer et al., 2011; Fisher et al., 2021; Fu & Waldman, 2019; Ghosh et al., 2021; O'Hanlon et al., 2018). The geographical distributions of these lineages vary globally, and inter-lineage contact zones appear to generate genetic mosaics, demonstrating the existence of inter-lineage recombination (Byrne et al., 2019; Jenkinson et al., 2016; O'Hanlon et al., 2018).

Amphibians in South Africa are known to be parasitized by two lineages of *Bd*—the globally widespread *Bd*GPL and rarer *Bd*CAPE which is largely found in Western and Southern Africa (Doherty-Bone et al., 2020; Ghosh & Fisher, 2016). The African continent is unusual with respect to *Bd* genomic diversity, as both lineages are widespread, and it is the globally rarer lineage, *Bd*CAPE, that has been shown to be the cause of amphibian mortality and population declines (Weldon et al., 2020). Environmental niche modeling has correlated *Bd* distribution in South Africa with cooler, wetter areas including where these conditions prevail for river catchments in predominantly dry regions (Tarrant et al., 2013). Disease surveillance within these regions of high environmental suitability for occurrence have subsequently revealed an overlapping distribution of these two lineages (Ghosh et al., 2021). Of conservation concern is the tendency of recombinant fungal pathogens to be more virulent than either of the parent lineages, to result in expanded host ranges (Brasier, 2000; Jenkinson et al., 2016; Walker et al., 2011), or to widen their geographical niche through the generation of diverse traits.

Here, we describe a multi-year broad-scale molecular genetic surveillance of *Bd* utilizing lineage-specific markers and genomic epidemiology. We focus on the Orange River system which spans a wide environmental gradient across altitude, temperature, and rainfall, and is commonly inhabited by frogs of the genus *Amietia*, all of which are known to be readily infected with *Bd* (Griffiths et al., 2018; Smith & Weldon, 2007; Weldon & Du Preez, 2006). Our analyses identify a suite of abiotic environmental factors that are associated with the distribution of *Bd* lineages and identifies a zone of lineage co-occurrence and inter-lineage recombination. This study therefore presents an opportune use of pathogen landscape genetics and ecological niche modeling to understand emergent patterns of pathogen distributions that can lead to disease.

2 | MATERIALS AND METHODS

2.1 | Field sampling

The Orange River was selected as a natural transect for this survey as it runs approximately 2300 km from the origin in the Lesotho highlands to the mouth at Alexander Bay where it enters the Atlantic Ocean (Lange et al., 2007). The river crosses cooler, summer rainfall regions at the origin, to the arid and warmer region along the western coast of South Africa (Cambray et al., 1986; Conley & Van Niekerk, 2000).

Field sites were focused on wetlands and other water bodies along the Orange River basin. There were 32 sites in total located across 1500 km from Vioolsdrift, at 155 m elevation at the most western site of the transect, to Lotheni in the Ukhamlamba Drakensberg National Park, at 1600 m elevation and the most eastern site of the transect. Areas where sites allowed for multiple sampling option within a 10 km radius were treated as single sites. At these sites, tadpoles and adult amphibians were collected by using dipnets or catching them by hand, respectively.

DNA was collected from the ventral surface of adult amphibians using sterile swabs, as well as from toe-clips from adult frogs for *Bd* isolation (Fisher et al., 2018). Tadpoles were euthanized by submersion in MS-222 solution (0.2%) before mouthparts were excised and preserved in 70% ethanol or used for *Bd* isolation (Fisher et al., 2018). Because the range of the study area did not allow for a

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

single species to be selected, sampling mostly focused on, but was not restricted to, members of the genus *Amietia* since it has representative species within the entire study area (Figure S1).

2.2 | Lineage identification of swab samples

Before lineage-specific qPCRs were run on field swab samples, we ran a pan-lineage ITS-PCR to determine if samples were positive for *Bd* (Boyle et al., 2004). Samples that amplified in duplicate with a GE > 0.1 were then subjected to lineage-specific qPCR, with primers designed for *Bd*GPL and *Bd*CAPE, using methods developed by Ghosh et al. (2021). All samples were run in duplicate, with two negative controls (for which dH_2O replaced the sample), and quantitation standards, created from zoospores harvested from confirmed *Bd*GPL and *Bd*CAPE isolates (Ghosh et al., 2021; O'Hanlon et al., 2018).

2.3 | Genomic analysis of isolates

Isolates were whole genome sequenced (WGS) as part of the work published by O'Hanlon et al. (2018). Briefly, these isolates were extracted and purified DNA was quality assured prior to library preparation with the Illumina HiSeq™ high output V4 chemistry and sequenced on an Illumina HiSeq™ machine (125 + 125 bp paired-end). Sequenced reads were aligned back to the *Bd*JEL423 reference genome using BWA-mem (Li & Durbin, 2009) and variant detection was performed using freebayes version dbb6160 (Garrison & Marth, 2012). High-quality variants were filtered using vcftools (Li et al., 2009) by applying the filtration steps outlined in O'Hanlon et al. (2018). We then generated a multi-sample VCF of all South African isolates using vcftools (Danecek et al., 2011). The combined VCF file was used to generate a Minimum Spanning Network (MSN; showing the genetic distance, Nei, between isolates) and a Principal Coordinate Analysis (showing separation of lineages) and isolation by distance analyses for each lineage.

We created the MSN using the poppr package (v2.8.1); the Principal Coordinate Analysis was generated using the adegant package (v2.1.1) and visualized using ggplot2 (v3.1.0). The isolation by distance analyses shows the correlation between geographic (Euclidian) distance and genetic distance (Nei) for each lineage. Euclidian distances were calculated using the R function dist in the R stats package (v3.5.1), and the genetic distance Nei, which assumes that genetic distance arises due to mutation and genetic drift, was calculated using the StAMPP package (v1.5.1). A Mantel test was carried out to assess if correlations between the genetic and geographic distances were statistically significant. An isolation by distance (IBD) model assumes genetic differentiation as a function of distance with a high R^2 value indicating that genetic distance and geographic distance are correlated. IBD does not consider any geographic complexity that may predict population structure and is used here as exploratory baseline analysis to investigate whether either lineage deviates from a simple genetic distance/geographical distance correlation.

2.4 | Site climate characterization

We characterized all *Bd* positive sites in terms of mean temperature (average daily surface temperature between 1981 and 2018), mean daily precipitation (per day averaged from 1981 to 2018), and mean annual dew/frost point at 2 m above ground level (daily average between 1981 and 2018). Mean temperature, mean daily precipitation, and mean annual dew point (https://power.larc.nasa.gov) were selected based on previous work by Puschendorf et al. (2009), Tarrant et al. (2013), and Murray et al. (2011). The MERRA-2 database was used to obtain data for these parameters with a resolution of 0.5° × 0.625° lat/lon calculating to approximately 50 km latitudinal distance. Kruskal-Wallis tests were used to determine if significant differences could be found between the medians of the environmental parameter groups, elevation, as well as prevalence at sites with *Bd*, due to data having a non-normal distribution. These tests were done with the environmental parameters per site in order to determine if sites were significantly different where the different lineages were found. Elevation was predicted to correlate with other variables, so we used a Pairwise Wilcox test on significantly different variables to identify groups that differed from each other, using Holm as the *p*-value adjustment method. The Merra-2 dataset was used due to its public availability, which allowed for the initial characterization of the general environmental envelope per lineage.

2.5 | Predictive distribution modeling

Initially the Merra-2 database was used to do site characterization of the *Bd* lineages found. This allowed for the rough characterization of areas suitable with the needs of the different lineages. After sampling along a transect spanning both lineages' climatic envelope, the results were used to construct lineage distribution models, using the finer scale information available from WorldClim (https://www.worldclim.org/data/bioclim.html).

We modeled lineage distributions using MaxEnt (version 3.4.4; Phillips et al., 2006) described by Elith et al. (2011) to correlate environmental parameters with the presence of either *Bd* lineage. A database was constructed from the records of *Bd* sampling in South Africa (accessible on the DRYAD database), but for the models, only positive sites were used with duplicate coordinates removed. Several studies have demonstrated the effectiveness of MaxEnt as a distribution modeling approach (Gibson et al., 2007; Hernandez et al., 2008; Pearson et al., 2007; Phillips et al., 2006; Stabach et al., 2009; Ward, 2007). In comparative analyses, MaxEnt has been shown to either outperform or perform comparably to models such as BIOCLIM, generalized linear models, random forest, support-vector machine, and DOMAIN (Yudaputra et al., 2019), as well as

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

to ensemble approaches combining random forest, support-vector machine, MaxLike, boosted regression trees, classification and regression trees, flexible discriminant analysis, and generalized linear models (Kaky et al., 2020).

A database for all known *Bd* records for South Africa, Lesotho, and Eswatini was created with the following information: locality and coordinates of sample origin, sample size, prevalence of *Bd*, lineage found (if available), date of sampling, and host genus and species name, with multiple samples seen as a single entry. Bioclimatic variables (30 s resolution) as well as the SRTM elevation dataset (30 s resolution) used for modeling were obtained from WorldClim (https://www.worldclim.org/data/bioclim.html). Prior to modeling, these variables were tested for inter-correlations, and only those exhibiting a correlation coefficient below the threshold of 0.7 were included in the analysis to ensure model robustness.

The use of the MaxEnt for predicting species' geographical distribution often involves default parameters, which could lead to complex and potentially overfitted models that are challenging to interpret, as highlighted by Radosavljevic and Anderson (2014) and Warren et al. (2014). To address this, Muscarella et al. (2014) introduced the R package ENMeval, which optimizes MaxEnt model parameters by assessing various combinations of regularization multipliers and features through metrics like AUC, AICc, and omission rates to mitigate overfitting. This approach facilitates the selection of model parameters that yield less complex models, thereby enhancing the reliability of the results and avoiding the biases that may arise from unvalidated user-selected parameters.

We used the ENMeval package within R version 4.0.2 to test for model parameters. This package was employed to assess an array of regularization multipliers (RM) alongside five feature types—linear (L), quadratic (Q), hinge (H), product (P), and threshold (T)—as per Phillips et al. (2006), with the model's fit and complexity judged by the corrected Akaike information criterion (AICc), while the AUC difference and 10% training omission rate gauged the potential overfitting (Akaike, 1973; Burnham & Anderson, 2004). The optimal parameter set for constructing each model was identified by the lowest delta.AICc value. For both the *Bd*GPL and *Bd*CAPE models, this meant an RM of 0.5 with features LQ (Tables S2 and S3).

The two models were subsequently executed using MaxEnt, wherein for each, a random subset constituting 80% of the positive instances was employed for training purposes, and the remaining 20% was utilized to validate the precision of the model's predictive capabilities. Model iterations were configured to 100 replications using the subsample method, with the random seed option activated to ensure reproducibility, while all other parameters were retained at their default values.

Model performances were evaluated using the area under curve (AUC) of the receiving operating characteristic (ROC) curve and by using jack-knife tests. The jack-knife tests examined the importance of each variable, firstly by removing one variable at a time and secondly by testing each variable in isolation (Figures S1 and S2). AUC values of 1 indicates perfect models, while values of 0.5 indicates that the model has no predictive ability. The "10 percentile training presence logistic threshold" was used to distinguish between suitable and non-suitable areas (*Bd*GPL = 0.1211; *Bd*CAPE = 0.0819), while the suitable areas were classified in to five suitability classes using a Natural Breaks (Jenks) method. The highest class of suitability for *Bd*GPL and *Bd*CAPE were then overlaid and further assessed.

3 | RESULTS

3.1 | *Bd* lineage abundance and distribution

The lineage of 204 samples (from the total positive samples of 270 that included 59 samples that were collected before 2015 fieldwork) were determined through lineage-specific qPCR of which approximately 72% of samples belonged to the *Amietia* genus. The most abundant species was *Amietia delalandii* ($n = 99$), while other species belonging to this genus accounted for the remaining 54 individuals (full species list in Table S1). In addition, 40 *Bd* isolates were cultured and subjected to whole genome sequencing (O'Hanlon et al., 2018). Collected isolates that were whole genome sequenced were either *Bd*CAPE, *Bd*GPL, or a recombinant lineage. This recombinant was identified using isolate clustering through principal component analyses using a subset of 3900 SNPs (O'Hanlon et al., 2018). In total, 17.78% of positives samples were identified to be *Bd*GPL, 47.41% determined to be *Bd*CAPE, 10.37% tested positive for both lineages, and 24.44% of positives could not be defined to lineage level. These unspecified positive samples were all part of the historical sample matrix and were collected prior to 2002, at which time isolation of cultures were not a focus for the sampling strategies, and lineage specific primers were not yet available.

In total, we described six *Bd*GPL-positive sites, 16 *Bd*CAPE-positive sites, and six sites from which we collected either a recombinant isolate, recovered both lineages, or detected both lineages at a single site via qPCR lineage-testing. A zone of regular lineage co-occurrence was detected in the Northern Cape Province, another co-occurrence zone was associated with the Drakensberg, and a third zone was detected in northern Limpopo (Figure 1).

3.2 | Lineage association with climate

Single lineage sites differed in mean annual temperature, mean daily precipitation, and elevation ($p < .05$). Wilcoxon Rank Sum tests revealed significant differences in mean annual temperature and mean annual precipitation for *Bd*CAPE-positive sites, compared to those that were positive for *Bd*GPL ($p < .0001$ and $p = .0055$, respectively) or both lineages ($p = .0146$ and $p = .0002$, respectively), but the same significant difference was not detected when comparing the mixed lineage sites to the *Bd*GPL-positive sites ($p = .2078$ and $p = .2365$, respectively). Concerning elevation, *Bd*CAPE compared with *Bd*GPL, as well as *Bd*GPL compared with mixed lineage sites, differed significantly ($p < .0001$ and $p = .0057$, respectively). Mixed lineage sites

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

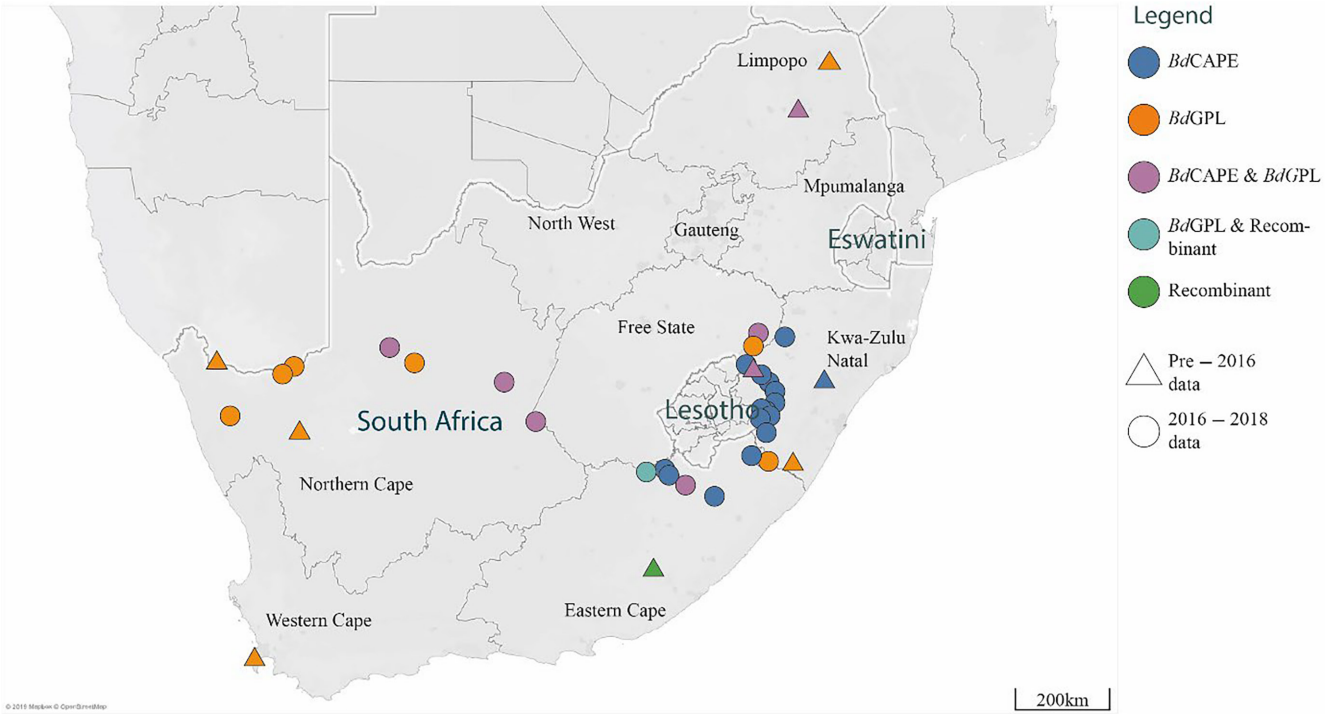
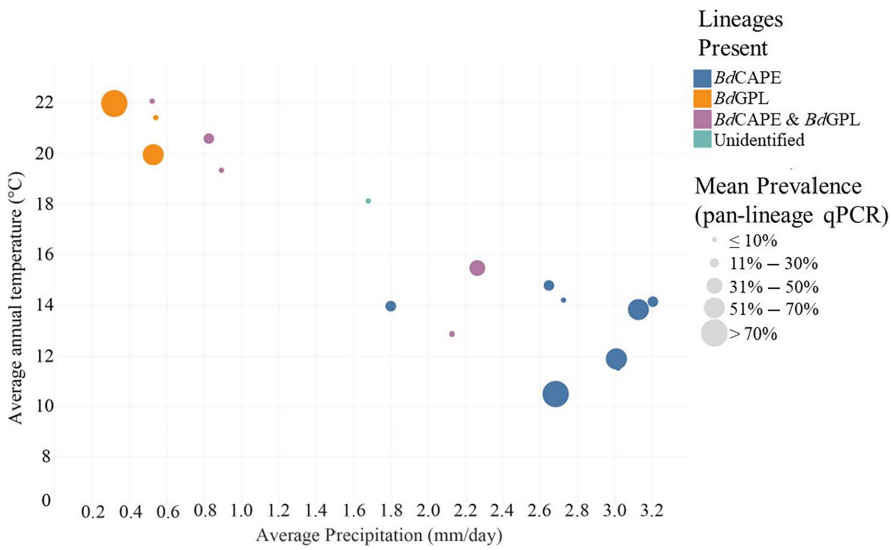


FIGURE 1 Distribution of *Bd* by lineage, indicating sites where both *Bd*GPL and *Bd*CAPE co-occur (*Bd*CAPE and *Bd*GPL, as well as *Bd*GPL and Recombinant, signifies sites where both lineages were detected or isolated).

FIGURE 2 Scatterplot showing qPCR lineage-typed sites according to average annual daily temperature and average annual daily precipitation.



were, however, not significantly different from *Bd*CAPE positive sites ($p = .1815$).

Generally, *Bd*GPL was found in drier, warmer sites (Figure 2). The range of environmental parameters where *Bd*GPL occurred was wider than for *Bd*CAPE. Conversely, *Bd*CAPE occurrence was correlated with high precipitation, and low-temperature environments. One exception was a *Bd*GPL isolate that originated from a more typical *Bd*CAPE area (Figure 1). When considering our data as visualized in Figure 2, it is apparent that the two basic lineages in South Africa have different core distributions separated by mean annual temperature and mean annual precipitation.

3.3 | Lineage population structures

The MSN revealed greater clonality among *Bd*GPL isolates compared with *Bd*CAPE isolates (Figure 3a). The IBD analyses (Figure 3b, c) reveal that *Bd*GPL shows strong isolation by distance, with an R^2

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

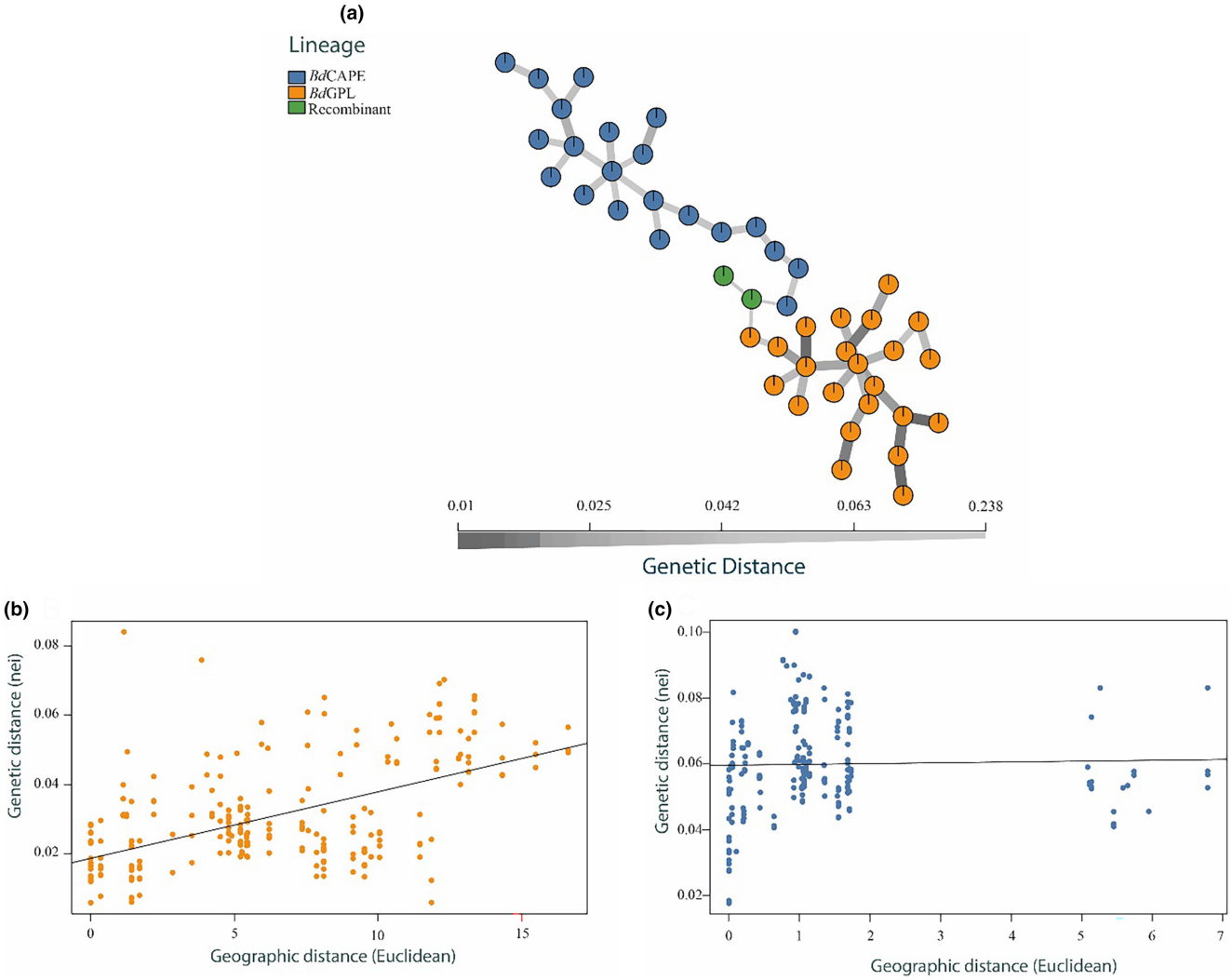


FIGURE 3 Comparative genomic analyses of *Bd* lineages (a) Minimum Spanning Network showing genetic distance between isolates. Closer genetic relatedness is illustrated by darker and thicker connecting lines between nodes, which represent individual isolates, (b) IBD plot for *Bd*GPL ($R^2 = .31$; $p < .05$), and (c) IBD plot for *Bd*CAPE ($R^2 < .05$; $p > .05$).

value of .31 ($p < .05$). Conversely, *Bd*CAPE shows evidence of a more complex population structure with the isolates falling into two clusters and no significant correlation between genetic and geographic distance ($R^2 < .05$, $p > .05$). The two *Bd*CAPE genetic clusters are also temporally and geographically clustered, so further work will be required to resolve whether this is a compounding sampling effect or the results of a reproductive barrier.

3.4 | Predicted *bd* lineage distribution

The database we constructed contained 1846 samples, originating from 48 species, 270 of which were positive records for *Bd*. Forty-eight of the positive samples belonged to the *Bd*GPL, 128 samples to *Bd*CAPE, and 28 samples tested positive for both *Bd*GPL and *Bd*CAPE. Lineage had not been assigned for the remaining 66 positive samples. The lineage-specific predicted distribution maps show that *Bd*CAPE has a restricted distribution, largely in eastern and southern coastal South Africa (Figure 4a). *Bd*GPL has an almost complete predicted distribution in South Africa including all areas where *Bd*CAPE is predicted to occur (Figure 4b). However, in the predicted hotspot for *Bd*CAPE, the eastern Great Escarpment, the environment is predicted to be highly suitable to *Bd*GPL (predicted above the threshold value of 0.1211—Figure 4b). Both models were strongly supported (*Bd*CAPE AUC: 0.968, *Bd*GPL AUC: 0.926). Analysis of the contribution of variables to the model showed that *Bd*GPL and *Bd*CAPE distributions were determined by different combinations of variables for both. The *Bd*CAPE model was influenced the most by the mean temperature of the driest quarter (at 54.2% contribution), while for *Bd*GPL, maximum temperature of the warmest month played the largest role (at 52.8%; Table 1). The resulting overlay of distribution indicated that the regions where both lineages include parts of Lesotho, the central and northern Drakensberg, the Eastern Cape, and south-western KwaZulu-Natal (Figure 4c).

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

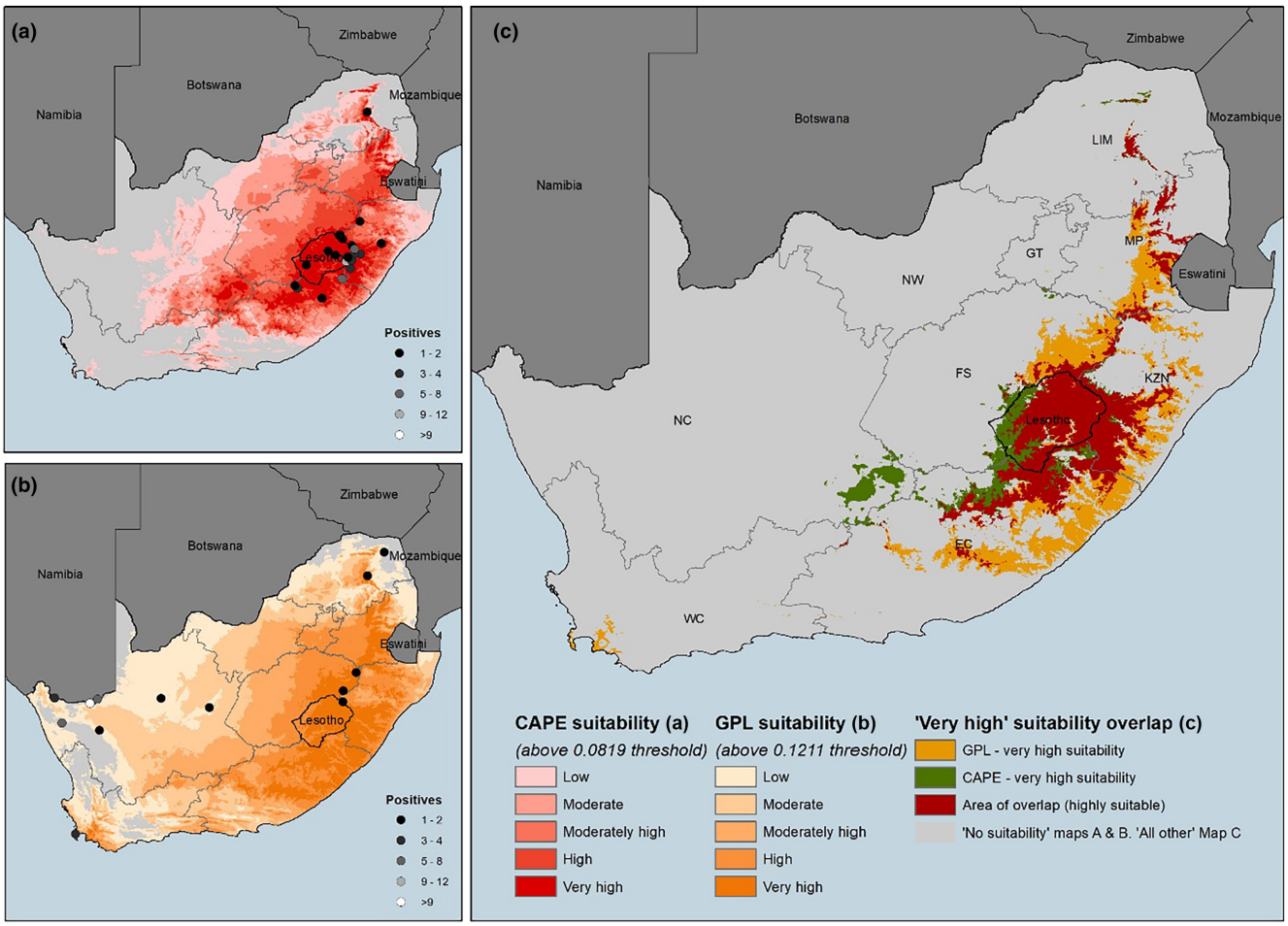


FIGURE 4 Suitability Maps for *Bd*CAPE (a) and *Bd*GPL (b). The "10th percentile training presence logistic threshold" is employed to differentiate between suitable and non-suitable areas. Subsequently, suitable areas are divided into five categories using the Natural Breaks (Jenks) method. Map (c) illustrates the regions where both lineages have areas of very high suitability. South African Provinces: WC, Western Cape; NC, Northern Cape; EC, Eastern Cape; FS, Free State; NW, North West; GT, Gauteng; LIM, Limpopo; MP, Mpumalanga; KZN, Kwazulu-Natal.

4 | DISCUSSION

Out data showed that *Bd* lineages in South Africa are largely separated by environmental niche, with multiple co-occurrence zones but only a single zone of overlap. *Bd*GPL was predominantly associated with low altitude environments that have a warmer, drier climate, and *Bd*CAPE mostly associated with cooler, higher precipitation environments. Both lineages show the potential for broader ecological niches as they sporadically occur within the opposing environmental envelope. It is within the contact zones that recombinant genotypes are expected to originate due to the higher frequency of mating opportunities between lineages.

For two fungal lineages to coexist, certain key factors are required such as sharing or partitioning of nutrients to reduce competition, spatial distribution (e.g., different lineages on separate hosts), or subtle differences in their physiological optimum that lead to seasonally driven temporal partitioning. Whatever facilitates coexistence, recombinant lineages may emerge because of sexual reproduction between lineages. These interactions among *Bd* lineages are rare and have only been described from surveillance and isolation efforts of *Bd* in South Africa and Brazil (Jenkinson et al., 2016; O'Hanlon et al., 2018; Schloegel et al., 2012). This stands in sharp contrast to the purported origin of amphibian associated chytrid fungi (AACs), Asia, where the greatest diversity of lineages has been identified but where no recombinants have been detected (O'Hanlon et al., 2018). *Bd* outside of Asia is an invasive pathogen, so areas of lineage overlap and recombination among lineages may be an outcome of anthropogenic globalization of AACs. Our data concur with previous studies showing that *Bd*GPL is less genetically diverse than *Bd*CAPE. The apparent presence of two clusters within the *Bd*CAPE population suggests at least two introduction events and perhaps some degree of reproductive barrier between sites of introduction, possibly due to altitudinal variation. However, the pattern may also be an artifact of sampling, which further surveillance could resolve. The observation of genetic isolation-by-distance for *Bd*GPL suggests that no reproductive barriers exist within their population, and points to what is likely a single introduction event; however, relatively low rates of gene flow with stepping-stone dispersal

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Bioclimatic variable contributions to the *Bd* lineage distribution models.

Key	Variable	Contribution to model	
		*Bd*GPL (%)	*Bd*CAPE (%)
Bio2	Mean Diurnal Range (Mean of monthly (max temp−min temp))	0.5	1.6
Bio3	Isothermality (BIO2/BIO7) (×100)	0.3	0.8
Bio5	Max Temperature of Warmest Month	52.8	15.9
Bio8	Mean Temperature of Wettest Quarter	0.6	1.1
Bio9	Mean Temperature of Driest Quarter	5.3	54.2
Bio11	Mean Temperature of Coldest Quarter	3.5	10.9
Bio13	Precipitation of Wettest Month	0.6	3.2
Bio14	Precipitation of Driest Month	5.1	0.8
Bio15	Precipitation Seasonality (Coefficient of Variation)	8.4	2.9
Bio19	Precipitation of Coldest Quarter	13.2	3.2
elev	Elevation above sea level	9.7	5.2

from a single point of origin, unimpeded by geographical or environmental barriers, suggests reduced opportunity for intralineage recombination. This observation may also suggest that *Bd*GPL was more recently introduced into South Africa.

However, where contact zones are generated, recombination is a key process for generating genetic diversity in fungi, from which *Bd* is no exception. Most often recombination in fungi occurs during meiosis, but phenotypic or genetic characteristics associated with meiosis have yet to be described for *Bd*. Rather the presence of widespread chromosomal copy number variation suggests some form of parasexual recombination drives recombinant formation (Farrer et al., 2013; James et al., 2015). A likely outcome of genetic recombination regardless of the mechanism of reproduction is that it allows for adaptation to changing environments, especially since the recombinant we recovered was found in an ecotone area between the predominant sites of the parental lineages. The recombinant lineages may very well be better adapted to the ecotonal area than either of the parental lineages, but that may also mean that it may be less adapted to the home ranges of either or both parental lineages. Future experimental work to test virulence and transmission under different climatic conditions can provide further clarification.

Overall, genetic recombination in fungi requires the presence of compatible mating types, specific environmental conditions, physical proximity between individuals, and the recognition and fusion of gametes (Ni et al., 2011; Taylor et al., 1999). When conditions are favorable during sexual reproduction, the haploid nuclei of two different individuals must recognize and fuse with one another to form a diploid zygote. This requires the production of specialized structures, such as fruiting bodies or gametangia, that allow the gametes to come into contact and fuse. Although *Bd* is speculated to have similar structures, evidence of their existence has not been found and await discovery. Nevertheless, the recent discovery of recombinants in *Bd* validates that compatibility exists between multiple lineages but what constitutes the required environmental conditions for recombination in *Bd* has not been defined. Our data revealed ample evidence for lineages being in close proximity to one another, either at the same site within the same host population or on the same host. The region of recombination in South Africa emulates an ecotone where the area dominated by *Bd*CAPE transitions into a *Bd*GPL-dominated area. Within this taxonomically defined geographical demarcation, both lineages are confronted by environmental change imposed by differences in climate. Within this area, the suitability of the environment means that the likelihood of individual lineages being brought into physical contact, through the actions of amphibians or through the inherent motility of zoospores, is increased. What the long-term consequences of genetic recombinants entails for the conservation of wild amphibian populations have yet to be determined. However, an in vitro challenge experiment found that the *Bd*GPL and *Bd*ASIA-2/BRAZIL recombinant was more virulent toward native hosts than either parental lineage (Greenspan et al., 2018).

Our landscape-scale analysis of *Bd* lineages in South Africa underscores the need to concentrate future genetic epidemiology on contact zones where both lineages occur in order to further understand the consequence of recombination on epidemiologically relevant traits. More widely, there is a clear need to widen surveillance to areas predicted to be suitable for the establishment of *Bd* in order to assess the risk that this pathogen poses to amphibians in Africa.

AUTHOR CONTRIBUTIONS

Ruhan Verster: Conceptualization (equal); investigation (equal); methodology (equal); project administration (equal); validation (supporting); visualization (supporting); writing – original draft

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(lead); writing – review and editing (equal). **Pria Natalia Ghosh:** Conceptualization (equal); data curation (equal); formal analysis (equal); visualization (equal); writing – review and editing (equal). **Tom R Sewell:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); visualization (equal); writing – review and editing (equal). **Trenton W. J. Garner:** Conceptualization (equal); funding acquisition (equal); writing – review and editing (equal). **Matthew Fisher:** Conceptualization (equal); funding acquisition (equal); writing – review and editing (equal). **Wynand Muller:** Visualization (equal); writing – review and editing (equal). **Dirk Cilliers:** Visualization (equal); writing – review and editing (equal). **Weldon Che:** Conceptualization (equal); project administration (lead); resources (equal); supervision (lead); writing – review and editing (lead).

ACKNOWLEDGMENTS

This study was approved by the Animal Research Ethics Committee of the North-West University (NWU ethics number: NWU-00015-16-S5). All animal collection for this study in the Northern Cape province of South Africa sampling was done under a Research permit from provincial government (Permit number: FAUNA 0539/2016). Data from animals in other parts of South Africa were obtained as historical data from co-authors. MCF is a fellow of the CIFAR Fungal Kingdoms program and receives funding from NERC NE/S000844/1 and MRC MR/R015600/1. TWJG is supported through funding from Research England and for this body of work grants from NERC (NE/S000992/1 and NE/K012509/1).

DATA AVAILABILITY STATEMENT

The dataset used for the predictive model was obtained from publications and our fieldwork and is available from the DRYAD database link in the Appendix. All the authors have no conflict of interest to declare.

ORCID

Ruhan Verster https://orcid.org/0000-0003-2974-1155

REFERENCES

Akaike, H. (1973). Maximum likelihood identification of gaussian autoregressive moving average models. *Biometrika*, *60*(2), 255–265.

Boyle, D. G., Boyle, D. B., Olsen, V., Morgan, J. A. T., & Hyatt, A. D. (2004). Rapid quantitative detection of chytridiomycosis (*Batrachochytrium dendrobatidis*) in amphibian samples using real-time Taqman PCR assay. *Diseases of Aquatic Organisms*, *60*, 141–148. https://doi.org/10.3390/s130708551

Brasier, C. (2000). The rise of the hybrid fungi. *Nature*, *405*(6783), 134–135. https://doi.org/10.1038/35012193

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Byrne, A. Q., Vredenburg, V. T., Martel, A., Pasmans, F., Bell, R. C., Blackburn, D. C., Bletz, M. C., Bosch, J., Briggs, C. J., Brown, R. M., Catenazzi, A., López, M. F., Figueroa-Valenzuela, R., Ghose, S. L., Jaeger, J. R., Jani, A. J., Jirku, M., Knapp, R. A., Stark, T., … Rosenblum, E. B. (2019). Cryptic diversity of a widespread global pathogen reveals expanded threats to amphibian conservation. *Proceedings of the National Academy of Sciences*, *116*(41), 20382–20387. https://doi.org/10.1073/pnas.1908289116

Cambray, J. A., Davies, A. J., Ashton, P. J., Agnew, J. D., De Moor, F. C., & Skelton, P. H. (1986). The Orange-Vaal river system. In B. R. Davies & K. F. Walker (Eds.), *The ecology of river systems* (pp. 89–161). Springer.

Conley, A. H., & van Niekerk, P. H. (2000). Sustainable management of international waters: The Orange River case. *Water Policy*, *2*(1–2), 131–149. https://doi.org/10.1016/s1366-7017(99)00026-4

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., Durbin, R., & 1000 Genomes Project Analysis Group. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*(15), 2156–2158. https://doi.org/10.1093/bioinformatics/btr330

Doherty-Bone, T., Cunningham, A., Fisher, M., Garner, T., Ghosh, P., Gower, D., Verster, R., & Weldon, C. (2020). Amphibian chytrid fungus in Africa–realigning hypotheses and the research paradigm. *Animal Conservation*, *23*(3), 239–244. https://doi.org/10.1111/acv.12538

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Farrer, R. A., Henk, D. A., Garner, T. W., Balloux, F., Woodhams, D. C., & Fisher, M. C. (2013). Chromosomal copy number variation, selection and uneven rates of recombination reveal cryptic genome diversity linked to pathogenicity. *PLoS Genetics*, *9*(8), e1003703. https://doi.org/10.1371/journal.pgen.1003703

Farrer, R. A., Weinert, L. A., Bielby, J., Garner, T. W. J., Balloux, F., Clare, F., Bosch, J., Cunningham, A. A., Weldon, C., du Preez, L. H., Anderson, L., Kosakovsky Pond, S. L., Shahar-Golan, R., Henk, D. A., & Fisher, M. C. (2011). Multiple emergences of genetically diverse amphibian-infecting chytrids include a globalized hypervirulent recombinant lineage. *Proceedings of the National Academy of Sciences*, *108*(46), 18732–18736. https://doi.org/10.1073/pnas.1111915108

Fisher, M. C., Ghosh, P., Shelton, J. M. G., Bates, K., Brookes, L., Wierzbicki, C., Rosa, G. M., Farrer, R. A., Aanensen, D. M., Alvarado-Rybak, M., Bataille, A., Berger, L., Böll, S., Bosch, J., Clare, F. C., Courtois, E. A., Crottini, A., Cunningham, A. A., Doherty-Bone, T. M., … Garner, T. W. J. (2018). Development and worldwide use of non-lethal, and minimal population-level impact, protocols for the isolation of amphibian chytrid fungi. *Scientific Reports*, *8*(1), 7772. https://doi.org/10.1038/s41598-018-24472-2

Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L., & Gurr, S. J. (2012). Emerging fungal threats to animal, plant and ecosystem health. *Nature*, *484*(7393), 186–194. https://doi.org/10.1038/nature10947

Fisher, M. C., Pasmans, F., & Martel, A. (2021). Virulence and pathogenicity of chytrid fungi causing amphibian extinctions. *Annual Review of Microbiology*, *75*, 673–693. https://doi.org/10.1146/annurev-micro-052621-124212

Fu, M., & Waldman, B. (2019). Ancestral chytrid pathogen remains hypervirulent following its long coevolution with amphibian hosts. *Proceedings of the Royal Society B*, *286*(1904), 20190833.

Garrison, E., & Marth, G. (2012). *Haplotype-based variant detection from short-read sequencing*. arXiv Preprint arXiv:1207.3907.

Ghosh, P., & Fisher, M. C. (2016). Dr Jekyll and Mrs Hyde: Risky hybrid sex by amphibian-parasitizing chytrids in the Brazilian Atlantic forests. *Molecular Ecology*, *25*(13), 2961–2963. https://doi.org/10.1111/mec.13668

Ghosh, P. N., Verster, R., Sewell, T. R., O'Hanlon, S. J., Brookes, L. M., Rieux, A., Garner, T. W. J., Weldon, C., & Fisher, M. C. (2021). Discriminating lineages of *Batrachochytrium dendrobatidis* using

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

quantitative PCR. *Molecular Ecology Resources*, *21*, 1452–1459. https://doi.org/10.1111/1755-0998.13299

Gibson, L., Barrett, B., & Burbidge, A. (2007). Dealing with uncertain absences in habitat modelling: A case study of a rare ground-dwelling parrot. *Diversity and Distributions*, *13*(6), 704–713. https://doi.org/10.1111/j.1472-4642.2007.00365.x

Greenspan, S. E., Lambertini, C., Carvalho, T., James, T. Y., Toledo, L. F., Haddad, C. F. B., & Becker, C. G. (2018). Hybrids of amphibian chytrid show high virulence in native hosts. *Scientific Reports*, *8*(1), 9600. https://doi.org/10.1038/s41598-018-27828-w

Griffiths, S. M., Harrison, X. A., Weldon, C., Wood, M. D., Pretorius, A., Hopkins, K., Fox, G., Preziosi, R. F., & Antwis, R. E. (2018). Genetic variability and ontogeny predict microbiome structure in a disease-challenged montane amphibian. *The ISME Journal*, *12*(10), 2506–2517. https://doi.org/10.1038/s41396-018-0167-0

Harvey, W. T., Carabelli, A. M., Jackson, B., Gupta, R. K., Thomson, E. C., Harrison, E. M., Ludden, C., Reeve, R., Rambaut, A., COVID-19 Genomics UK (COG-UK) Consortium, Peacock, S. J., & Robertson, D. L. (2021). SARS-CoV-2 variants, spike mutations and immune escape. *Nature Reviews Microbiology*, *19*(7), 409–424. https://doi.org/10.1038/s41579-021-00573-0

Hernandez, P. A., Franke, I., Herzog, S. K., Pacheco, V., Paniagua, L., Quintana, H. L., Quintana, H. L., Soto, A., Swenson, J. J., Tovar, C., Valqui, T. H., Vargas, J., & Young, B. E. (2008). Predicting species distributions in poorly-studied landscapes. *Biodiversity and Conservation*, *17*, 1353–1366. https://doi.org/10.1007/s10531-007-9314-z

James, T. Y., Toledo, L. F., Rödder, D., da Silva Leite, D., Belasen, A. M., Betancourt-Román, C. M., Jenkinson, T. S., Soto-Azat, C., Lambertini, C., Longo, A. V., Ruggeri, J., Collins, J. P., Burrowes, P. A., Lips, K. R., Zamudio, K. R., & Longcore, J. E. (2015). Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: Lessons from the first 15 years of amphibian chytridiomycosis research. *Ecology and Evolution*, *5*(18), 4079–4097. https://doi.org/10.1002/ece3.1672

Jenkinson, T. S., Betancourt Román, C. M., Lambertini, C., Valencia-Aguilar, A., Rodriguez, D., Nunes-de-Almeida, C. H. L., Ruggeri, J., Belasen, A. M., da Silva Leite, D., Zamudio, K. R., Longcore, J. E., Toledo, F. L., & James, T. Y. (2016). Amphibian-killing chytrid in Brazil comprises both locally endemic and globally expanding populations. *Molecular Ecology*, *25*(13), 2978–2996. https://doi.org/10.1111/mec.13599

Kaky, E., Nolan, V., Alatawi, A., & Gilbert, F. (2020). A comparison between ensemble and MaxEnt species distribution modelling approaches for conservation: A case study with Egyptian medicinal plants. *Ecological Informatics*, *60*, 101150. https://doi.org/10.1016/j.ecoinf.2020.101150

Lange, G.-M., Mungatana, E., & Hassan, R. (2007). Water accounting for the Orange River basin: An economic perspective on managing a transboundary resource. *Ecological Economics*, *61*(4), 660–670. https://doi.org/10.1016/j.ecolecon.2006.07.032

Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with burrows-wheeler transform. *Bioinformatics*, *25*(14), 1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., & 1000 Genome Project Data Processing Subgroup. (2009). The sequence alignment/map format and SAMtools. *Bioinformatics*, *25*(16), 2078–2079. https://doi.org/10.1093/bioinformatics/btp352

Martel, A., Spitzen-van der Sluijs, A., Blooi, M., Bert, W., Ducatelle, R., Fisher, M. C., Woeltjes, A., Bosman, W., Chiers, K., Bossuyt, F., & Pasmans, F. (2013). *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. *Proceedings of the National Academy of Sciences*, *110*(38), 15325–15329. https://doi.org/10.1073/pnas.1307356110

Murray, K. A., Retallick, R. W. R., Puschendorf, R., Skerratt, L. F., Rosauer, D., McCallum, H. I., Berger, L., Speare, R., & VanDerWal, J. (2011). Assessing spatial patterns of disease risk to biodiversity: Implications for the management of the amphibian pathogen, *Batrachochytrium dendrobatidis*. *Journal of Applied Ecology*, *48*(1), 163–173. https://doi.org/10.1111/j.1365-2664.2010.01890.x

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MaxEnt ecological niche models. *Methods in Ecology and Evolution*, *5*(11), 1198–1205. https://doi.org/10.1111/2041-210X.12261

Ni, M., Feretzaki, M., Sun, S., Wang, X., & Heitman, J. (2011). Sex in fungi. *Annual Review of Genetics*, *45*, 405–430. https://doi.org/10.1146/annurev-genet-110410-132536

O'Hanlon, S. J., Rieux, A., Farrer, R. A., Rosa, G. M., Waldman, B., Bataille, A., Kosch, T. A., Murray, K. A., Brankovics, B., Fumagalli, M., Martin, M. D., Wales, N., Alvarado-Rybak, M., Bates, K. A., Berger, L., Böll, S., Brookes, L., Clare, F., Courtois, E. A., … Fisher, M. C. (2018). Recent Asian origin of chytrid fungi causing global amphibian declines. *Science*, *360*, 621–627. https://doi.org/10.1126/science.aar1965

Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Townsend Peterson, A. (2007). Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography*, *34*(1), 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Puschendorf, R., Carnaval, A. C., VanDerWal, J., Zumbado-Ulate, H., Chaves, G., Bolaños, F., & Alford, R. A. (2009). Distribution models for the amphibian chytrid *Batrachochytrium dendrobatidis* in Costa Rica: Proposing climatic refuges as a conservation tool. *Diversity and Distributions*, *15*(3), 401–408. https://doi.org/10.1111/j.1472-4642.2008.00548.x

Radosavljevic, A., & Anderson, R. P. (2014). Making better MaxEnt models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, *41*(4), 629–643. https://doi.org/10.1111/jbi.12227

Scheele, B. C., Pasmans, F., Skerratt, L. F., Berger, L., Martel, A., Beukema, W., Acevedo, A. A., Burrowes, P. A., Carvalho, T., Catenazzi, A., De la Riva, I., Fisher, M. C., Flechas, S. V., Foster, C. N., Frías-Álvarez, P., Garner, T. W. J., Gratwicke, B., Guayasamin, J. M., Hirschfeld, M., … Canessa, S. (2019). Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science*, *363*(6434), 1459–1463. https://doi.org/10.1126/science.aav0379

Schloegel, L. M., Toledo, L. F., Longcore, J. E., Greenspan, S. E., Vieira, C. A., Lee, M., Zhao, S., Wangen, C., Ferreira, C. M., Hipolito, M., Davies, A. J., Cuomo, C. A., Daszak, P., & James, T. Y. (2012). Novel, panzootic and hybrid genotypes of amphibian chytridiomycosis associated with the bullfrog trade. *Molecular Ecology*, *21*(21), 5162–5177. https://doi.org/10.1111/j.1365-294X.2012.05710.x

Smith, K. G., & Weldon, C. (2007). A conceptual framework for detecting oral chytridiomycosis in tadpoles. *Copeia*, *2007*(4), 1024–1028. https://doi.org/10.1643/0045-8511(2007)7%5B1024:ACFFDO%5D2.0.CO;2

Stabach, J. A., Laporte, N., & Olupot, W. (2009). Modeling habitat suitability for Grey crowned-cranes (*Balearica regulorum gibbericeps*) throughout Uganda. *International Journal of Biodiversity and Conservation*, *1*(5), 177–186.

Tarrant, J., Cilliers, D., Du Preez, L. H., & Weldon, C. (2013). Spatial assessment of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) in South Africa confirms endemic and widespread infection.

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

PLoS ONE, *8*(7), e69591. https://doi.org/10.1371/journal.pone.0069591

Taylor, J., Jacobson, D., & Fisher, M. (1999). The evolution of asexual fungi: Reproduction, speciation and classification. *Annual Review of Phytopathology*, *37*(1), 197–246. https://doi.org/10.1146/annurev.phyto.37.1.197

Walker, A. S., Bouguennec, A., Confais, J., Morgant, G., & Leroux, P. (2011). Evidence of host-range expansion from new powdery mildew (*Blumeria graminis*) infections of triticale (× *Triticosecale*) in France. *Plant Pathology*, *60*(2), 207–220. https://doi.org/10.1111/j.1365-3059.2010.02379.x

Ward, D. F. (2007). Modelling the potential geographic distribution of invasive ant species in New Zealand. *Biological Invasions*, *9*, 723–735. https://doi.org/10.1007/s10530-006-9072-y

Warren, D. L., Wright, A. N., Seifert, S. N., & Shaffer, H. B. (2014). Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distributions*, *20*(3), 334–343. https://doi.org/10.1111/ddi.12160

Weldon, C., Channing, A., Misinzo, G., & Cunningham, A. A. (2020). Disease driven extinction in the wild of the Kihansi spray toad. *Nectophrynoides Asperginis*. *African Journal of Herpetology*, *69*(2), 151–164. https://doi.org/10.1080/21564574.2020.1752313

Weldon, C., & Du Preez, L. H. (2006). Quantitative measurement of *Batrachochytrium dendrobatidis* in amphibian skin. *Diseases of Aquatic Organisms*, *72*(2), 153–161. https://doi.org/10.3354/dao072153

Yudaputra, A., Pujiastuti, I., & Cropper, W. P. (2019). Comparing six different species distribution models with several subsets of environmental variables: Predicting the potential current distribution of *Guettarda speciosa* in Indonesia. *Biodiversitas*, *20*(8), 2321–2328. https://doi.org/10.13057/biodiv/d200830

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Verster, R., Ghosh, P. N., Sewell, T. R., Garner, T. W. J., Fisher, M. C., Muller, W., Cilliers, D., & Weldon, C. (2024). Environment predicts *Batrachochytrium dendrobatidis* lineage distribution and zones of recombination in South Africa. *Ecology and Evolution*, *14*, e11037. https://doi.org/10.1002/ece3.11037

20457758, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1002/ece3.11037 by North-West University, Wiley Online Library on [20/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License