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Functional Trait Capacity: from observing biodiversity to predicting landscape capacity



Christopher John Topping^{1,2}✉, Tommy Dalgaard^{1,3,4}, Claus Rasmussen¹ & Yoko Luise Dupont¹

Current biodiversity metrics describe what is present, but struggle with what landscapes could sustain under alternative management. We define Functional Trait Capacity (FTC) as the biologically admissible strategies remaining viable under specified landscape, management and time-horizon conditions. A synthetic demonstration shows that identical observed communities can conceal different capacities and that the same intervention can create different gains. FTC links biodiversity state to ecological mechanism and prospective management.

The measurement problem in agricultural biodiversity

Biodiversity metrics have developed through three overlapping generations: species-based, functional-diversity and habitat-based metrics. Each has brought a real operational advance. Species-based indices describe realised community composition but provide no mechanism for prediction¹. Functional-diversity indices characterise the distribution of traits within existing communities, but still depend on inventories of the species already present². Habitat-based metrics replace species surveys with habitat classification, which greatly improves scalability and operational feasibility³.

At the global scale, the Kunming–Montreal Global Biodiversity Framework, adopted at COP15 in December 2022, formalises habitat-based measures within its biodiversity monitoring and reporting targets for 2030^{4,5}. England's statutory Biodiversity Net Gain requirement provides a jurisdiction-specific example. Mandatory from 2024 under the Environment Act 2021, it uses habitat distinctiveness and condition to calculate standardised biodiversity units⁶. The proxy is useful but incomplete: the metric is associated with measurable gains in plant biodiversity, but not in birds or butterflies⁷, and predicts invertebrate biodiversity poorly⁸.

The three generations nevertheless share the same structural limitation. They measure patterns in realised biodiversity rather than the processes that generate those patterns. The limitation also applies to ambitious proposals for observational monitoring. The European Biodiversity Observation Network roadmap⁹, for example, proposes 84 Essential Biodiversity Variables spanning genes to ecosystems. These variables can standardise how biodiversity state and change are measured, but they remain observational by design. They cannot provide the causal prediction needed to evaluate an individual management decision.

This leaves a question that agricultural policy, the Taskforce on Nature-related Financial Disclosures (TNFD) and farm management all need to answer: if management changes here, what happens to biodiversity capacity? Here, capacity means the range of ecological strategies that the landscape can support, rather than the set currently observed. Predicting how management changes that capacity is necessary for assessing progress towards the EU Biodiversity Strategy and Nature Restoration Regulation, among other policy goals. More observations alone cannot supply this prediction, because the missing element is a representation of the processes that produce biodiversity.

Biodiversity metrics are already used in prediction. Land-use models coupled to species distribution, joint species distribution and occupancy models project biodiversity under alternative scenarios, and spatially explicit models can reveal why agri-environment measures vary in effectiveness¹⁰. Our argument is narrower: these approaches do not predict biodiversity capacity. Because they are fitted to observed occurrences, they project associations between recorded species and recorded conditions. The projected species pool is bounded by the region and period used for fitting; transfer beyond that range is assumed rather than derived from mechanism; and the output is expected occurrence, not the conditions required for persistence. Consequently, such models cannot identify which ecological constraint prevents a management response from occurrence data alone. The demonstration below makes the distinction explicit. Four landscapes with the same constructed observed community differ in capacity by as many as 23 strategies. Those additional strategies occur in none of the observations and therefore cannot be recovered by a model fitted only to them. Mechanistic alternatives to correlative distribution modelling exist, and FTC belongs with these. The distinction is between observation-

¹Department of Agroecology, Aarhus University, Aarhus, Denmark. ²Social-Ecological Systems Simulation Centre, Aarhus University, Aarhus, Denmark. ³Center for Sustainable Landscapes under Global Change, Aarhus, Denmark. ⁴Present address: Land-CRAFT, Center for Landscape Research in Sustainable Agricultural Futures, Aarhus, Denmark. ✉e-mail: cjt@agro.au.dk

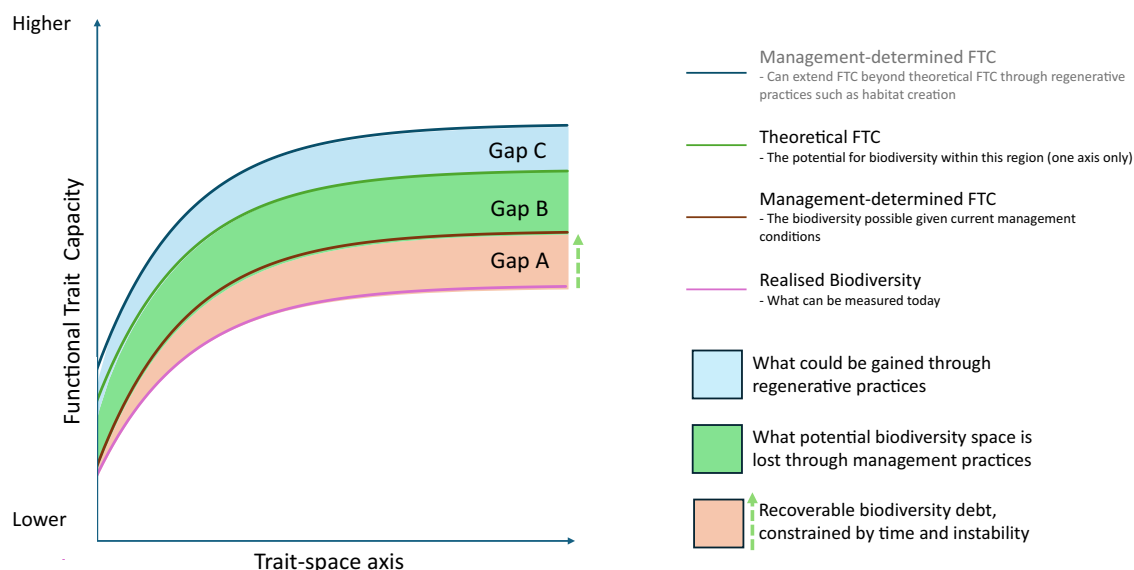


Fig. 1 | Three capacity states of Functional Trait Capacity (FTC) and the contrasts among them. Theoretical FTC is the capacity associated with an explicitly declared reference landscape or counterfactual. Management-determined FTC is the capacity under a specified land-use and management regime and may be lower or higher than that reference. Realised biodiversity is the historically filtered community

measurable at the time of observation and may lag behind current capacity. Management-induced gain is a scenario contrast, not a fourth capacity state. The gaps distinguish capacity lost or created by management from capacity that is viable but not yet realised.

anchored and mechanistic prediction, not between description and prediction.

The empirical pattern: why the same management produces different outcomes

Two decades of agri-environment scheme evaluation and farming-systems research have produced an inconsistent but poorly explained pattern^{11–13}: the same intervention gives different biodiversity responses in different landscape contexts, sometimes even in opposite directions. Organic farming and agri-environment schemes, two of the best-studied interventions in European agricultural landscapes, show the pattern clearly.

Meta-analyses indicate that organic management increases species richness by about 30% on average relative to conventional farming^{14,15}, yet 16% of studies report negative effects¹⁴. Benefits tend to be greater in intensively managed, structurally homogeneous landscapes than in heterogeneous ones, and responses differ among taxonomic and functional groups and crop types^{14–16}. A global analysis of 60 crops across six continents confirmed that ecological benefits were greatest in intensive agricultural landscapes, while also showing that the same landscape variable could have contrasting effects on different sustainability outcomes¹⁶.

Agri-environment schemes show the same dependence on context. Kleijn et al.¹³ found substantial variation among countries, taxa and scheme types, with common species benefiting more than species of conservation concern. Batáry et al.¹⁷ showed that landscape structure modified scheme effectiveness: species richness increased in simple cropland landscapes but not in complex ones. A later synthesis attributed effectiveness to the interaction among ecological contrast, land-use intensity and landscape context¹⁸. Yet schemes are still designed and evaluated largely with observational, species-specific metrics that contain no general mechanism for predicting these differences.

Spatially explicit analyses provide independent evidence for the same mechanism. Across 611 landscapes, landscape structure explained 84% of variation in simulated mean beetle density and 70% of variation in pesticide impact, while mitigation effects were also strongly landscape dependent¹⁹. These results support a capacity-based formulation, although they do not themselves test FTC.

The variable outcomes are therefore unlikely to be explained simply as failures of an intervention or its design. They arise because an intervention acts on biodiversity capacity, a property generated by the landscape as a system, whereas evaluation usually records species occurrence or abundance at particular places and times. A predictive metric must represent the processes that generate capacity, not only the patterns those processes have already produced.

The conceptual advance: Functional Trait Capacity

We define Functional Trait Capacity (FTC) as the range of viable functional-trait combinations that a landscape can sustain. The object of measurement is therefore ecological capacity rather than the community currently observed. FTC concerns the breadth of ecological strategies and life-history solutions for which the landscape provides viable conditions. A wider trait space can support a greater range of species and functional groups, because landscapes act on the resources, disturbance regimes and environmental constraints that select among trait combinations. Species composition is one historically contingent outcome of that filtering. FTC does not replace assessment of species of conservation concern; it answers a different, complementary question.

The formal and biological foundations already exist. Hutchinson's *n*-dimensional hypervolume provides a structure for representing the trait space accessible under specified conditions²⁰, while functional-trait ecology supplies the biologically meaningful axes along which capacity is expressed²¹. FTC joins these ideas by asking which trait combinations a landscape can sustain, rather than which combinations happen to be present. This change in the predicted object makes it possible to evaluate management scenarios before they are implemented.

We distinguish three capacity states (Fig. 1).

Theoretical FTC is the trait capacity expected from a site's physical characteristics and natural ecological trajectory in the absence of deliberate management. It is a declared reference, not an absolute biophysical maximum or a state that could necessarily be observed today. Long-transformed agricultural landscapes may retain no unmanaged analogue, in which case the reference must be modelled or defined as a scenario. Its provenance must accompany every FTC estimate because it determines the size of the gaps shown in Fig. 1.

Management-determined FTC is the capacity produced by a specified land-use and management regime, and is therefore the state that management can alter directly. It is not necessarily lower than theoretical FTC. Management may remove capacity, but it may also create conditions absent from the natural trajectory, for example by maintaining open habitat where woodland would otherwise develop or by creating aquatic habitat in a dry landscape. Such an increase is a management-induced gain relative to the declared reference.

Realised biodiversity is the community currently present after historical and ecological filtering. It should tend towards management-determined FTC through time, but may lag behind it. This is the state measured by existing observational metrics.

The differences among these states represent biodiversity debts or opportunities (Fig. 1). They separate capacity lost or created through management from capacity that is viable but has not yet been realised. This decomposition connects biodiversity assessment to the choices made by farmers, land managers and policymakers.

FTC is intended to work with observational systems. The EBV architecture described by Kissling et al.⁹ can track realised biodiversity state and trend across space and time. FTC asks the adjacent causal question: given specified landscape conditions and management, what functional capacity should result, and how does it compare with the observed community? Neither question substitutes for the other.

Why capacity matters for sustainable agriculture

Agricultural biodiversity is generated across connected landscapes; it is not allocated independently between production and conservation areas. Landscape composition, configuration and management together determine resource continuity, disturbance exposure, movement and demographic exchange^{22,23}. The relevant decision object is therefore the capacity of the whole landscape, including its farmed matrix. This is consistent with work on working landscapes and ecological intensification, both of which treat farmland as capable of supporting biodiversity^{24,25}. FTC adds an estimate of the capacity that a given management configuration can sustain.

The historical record supports this whole-landscape view. Biodiversity has continued to decline while protected-area coverage has expanded^{26–28}. Flying-insect biomass declined by more than 75% over 27 years in German nature reserves²⁹, and later work linked arthropod declines to surrounding agricultural intensity, pesticide exposure and edge effects^{30–32}. Spatially explicit population models likewise show how source–sink dynamics can conceal habitat inadequacy³³. These comparisons are not controlled experiments: protected areas are not randomly located with respect to land-use pressure, and monitoring is uneven across space and taxa³⁴. They nevertheless show why designation alone cannot define the capacity of the surrounding landscape.

FTC makes this a conditional capacity question. The same field- or landscape-level intervention can produce a large gain when it removes the binding limitation and little response when another constraint dominates. The calculation does not prescribe a conservation target. It estimates the ecological consequences of alternative choices after production, conservation and ecosystem-service goals have been specified^{35,36}. Land users, advisers and public bodies set those goals; goal setting therefore precedes capacity assessment and remains a participatory decision.

This distinction matters for the Kunming–Montreal Global Biodiversity Framework⁴, the EU Nature Restoration Regulation and forward-looking nature-risk assessment. These initiatives require choices about future outcomes, whereas observational indicators principally establish present state and trend. FTC supplies a scenario-conditioned estimate of what those choices could sustain.

Making FTC calculable: a minimal computational demonstration

A conditioned viable-strategy set

We define FTC as $FTC(L, M, H | Z, \theta)$, where L describes landscape configuration and state, M the management regime, H the assessment horizon,

Z the biologically admissible strategy space and θ the model parameters and thresholds. An FTC value is interpretable only when these conditions are declared. In the discrete demonstration described in Supplementary Note 1, FTC is the set of admissible virtual strategies that meet a specified persistence criterion. Each strategy represents a biologically coherent combination of traits, not a named taxon.

Model design and viability

We generated 80 strategies from 16 archetypes defined by four trophic roles, two fast–slow life-history classes and two disturbance-response classes, with five variants of each archetype. Four traits determine viability: spatial access, temporal resource requirement, disturbance tolerance and biotic dependency. Rules for phenological overlap, trophic consistency and downward, acyclic food-web dependencies exclude biologically arbitrary combinations.

The four 50×50 -cell agricultural landscapes form a 2×2 design that varies field configuration (16 or 64 fields) and non-crop area (5% or 20%). Five landscape components supply 24 half-monthly profiles of basal resources, habitat structure and disturbance. A producer is locally viable where resources, habitat and disturbance conditions remain suitable through its critical window. A consumer must also find viable food from the trophic level below within its circular spatial-access neighbourhood. We propagate viability from producers to tertiary consumers until no strategy changes state.

A strategy enters landscape FTC if it contains at least one four-neighbour-connected patch of 25 locally persistent cells. The threshold represents 1% of the landscape and is an experimental choice, not an empirical minimum-area requirement. The solver also records viable area and largest patch size, so alternative persistence thresholds can be tested without changing the underlying ecological calculation. Supplementary Note 1, Sections S1–S12, provides the equations, parameters, pseudocode and validation tests; the robustness analyses are reported in Sections S9 and S10.

Controlled comparison and common intervention

We first separated observed composition from capacity by selecting the same 32-strategy realised community from the strategies viable in all four reference landscapes. The matched set covers all 16 archetypes and trophic levels, and serves as an experimental control rather than a model of community assembly. We then applied the same intervention to each landscape: edge-first conversion of 5% of cropped cells to semi-natural herbaceous habitat, allocated among fields in proportion to their cropped area.

Demonstration results

We first asked whether landscapes with the same realised community could differ in capacity. The constructed community contained the same 32 strategies in all four landscapes, but assessment of all 80 admissible strategies gave FTC values of 46 in L1, 67 in L2, 44 in L3 and 65 in L4 (Fig. 2b). Identical realised richness therefore concealed a difference of as many as 23 viable strategies.

We then applied the common intervention. FTC increased from 46 to 60 strategies in L1 and from 44 to 48 in L3, but remained at 67 in L2 and 65 in L4 (Fig. 2c). Thus, the same conversion created capacity for 14 additional strategies in L1, four in L3 and none in L2 or L4. The absence of a richness change did not imply the absence of an ecological response. Mean viable area increased by 1.8–2.6 percentage points in every landscape, showing that the intervention could expand the area available to strategies already counted within FTC without enabling another strategy to cross the persistence threshold.

We next tested whether this result depended on the structural choices in the reference analysis. Persistence thresholds ranged from 1 to 100 connected cells, conversion intensity from 1 to 10% of cropped area, and converted cells were placed using three rules. These choices produced 60 combinations per landscape. At every persistence threshold, the high-non-crop landscape had greater FTC than its low-non-crop counterpart. FTC change differed among landscapes in 50 of the 60

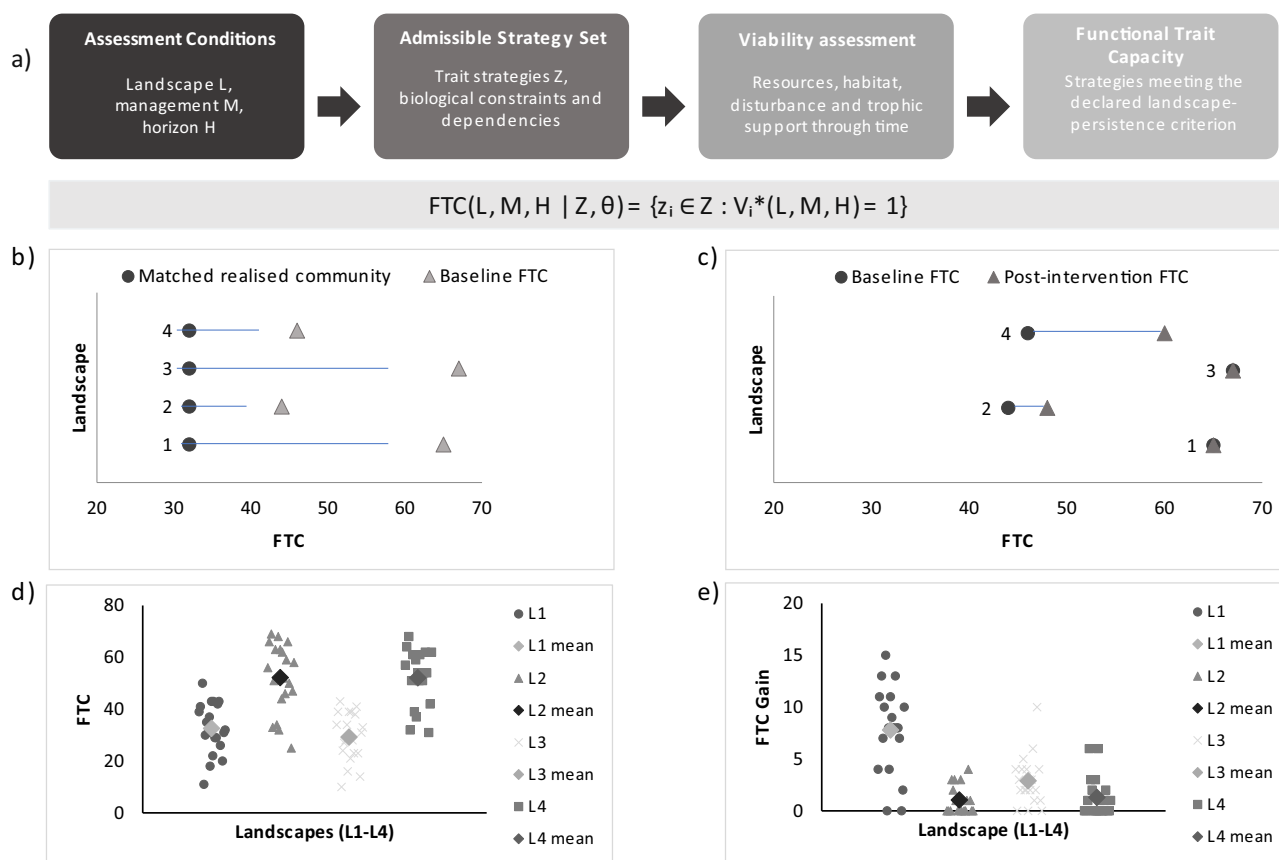


Fig. 2 | A computable demonstration of Functional Trait Capacity (FTC). **a** FTC is calculated as the subset of biologically admissible strategies that remains viable under declared landscape, management, assessment-horizon and parameter conditions. **b** In the deterministic reference case (seed 42), the same constructed, archetype-complete community of 32 strategies was selected from the strategies viable in all four landscapes. Despite this identical realised richness, baseline FTC differed among landscapes. **c** Baseline and post-intervention FTC following edge-first conversion of 5% of cropped cells to semi-natural herbaceous habitat. The intervention increased FTC by 14 strategies in Landscape 1 (L1) and four in L3, but produced no change in L2 or L4. **d** Distribution of baseline FTC across 20 combined

sensitivity replicates in which both the 80-strategy sample and bounded seasonal resource and disturbance profiles were varied. Each replicate used the same set of sampled strategies and seasonal profile draws across all four landscapes. Baseline FTC was unequal in every replicate, with L2 > L1 and L4 > L3 in 20/20 replicates. **e** Distribution of FTC change following the same intervention across those replicates. Intervention effects differed among landscapes in 20/20 replicates, demonstrating that the capacity gain was conditional on landscape context. Points represent individual replicates; larger symbols show means. L1 and L2 have large fields and respectively 5% and 20% non-crop habitat; L3 and L4 have small fields and respectively 5% and 20% non-crop habitat.

combinations, and viable area increased monotonically with conversion intensity in all 12 landscape-by-placement sequences. The context-dependent response was therefore not an artefact of the reference threshold, intensity or placement rule.

Finally, we varied the strategies and seasonal conditions used in the reference case. Three ensembles of 20 replicates changed the sampled strategies, the bounded seasonal resource and disturbance profiles, or both together. Baseline FTC differed among landscapes in every replicate, and the high-non-crop landscape always exceeded its low-non-crop counterpart (Fig. 2d). In all 20 combined replicates, the FTC response to intervention also differed among landscapes (Fig. 2e). The matched 32-strategy community in Fig. 2b is therefore an illustrative control. The robust results are the unequal landscape capacities and the dependence of intervention response on landscape context.

From computational demonstration to operational use

The demonstration shows that FTC can be calculated; it does not establish empirical validity. Observations are still required to parameterise resource use, movement, habitat requirements and disturbance responses, to test predicted viability and community composition, and to estimate uncertainty. Their role changes rather than disappears: observations inform and test the ecological processes, while the model uses those processes to predict viable strategies under conditions not yet observed.

Operational users should not need to run or inspect the process model. We envisage a process-based estimation layer that supplies maps, scenario contrasts, limiting-factor diagnoses and uncertainty-bounded indicators to an operational layer used by farm advisers, conservation managers and policy analysts. Whether this is adopted will depend as much on institutional fit as on ecological content. The inputs already correspond to established data streams: Integrated Administration and Control System (IACS) for cropping and management, remote sensing and habitat inventories for configuration, administrative records for field operations, and open compilations for traits. FTC outputs could therefore be reported at the units these systems already use, alongside existing indicators. Monitoring remains necessary because it supplies the realised state against which capacity estimates are tested. The estimation layer also need not be built from nothing. Spatially explicit platforms already represent resources, disturbance and habitat configuration under alternative management across European agricultural systems. The Animal Landscape and Man Simulation System (ALMaSS), for example, couples high-resolution dynamic landscapes to mechanistic population models and has been applied in eleven European countries^{37,38}. Such platforms belong behind the operational interface; an adviser or manager would not be expected to operate them. Methods for constructing their landscape representations from public EU geospatial data have been formalised and applied across member states³⁹. The method is transferable where the underlying layers exist, but this does not make

national management data equivalent, equally resolved or equally accessible. Three practical constraints remain. IACS records are not openly accessible in every member state; spatially explicit management data are often coarse or absent; and pesticide mixtures and habitat condition are incompletely represented. An operational product and its governance also remain to be demonstrated. Finally, context-specific advice already exists in many regions, yet uptake is constrained by administrative burden and cost. FTC could improve the evidence on which decisions are based, but cannot by itself remove these institutional barriers.

The next empirical step is to replace the experimental profiles and virtual-strategy ranges with taxon- and region-specific evidence. FTC predictions can then be tested against observed variation in management response and compared with realised-diversity and habitat-only baselines. The synthetic demonstration makes that test falsifiable by specifying which assumptions must be calibrated and which outputs must be compared.

Monitoring and FTC therefore have distinct roles. Monitoring establishes what is present and how it changes. FTC estimates what the landscape can sustain and how that capacity changes among management scenarios. Their combination connects observed biodiversity to ecological mechanism and prospective landscape decisions.

Data availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

Code availability

All programming code supporting the findings of this study is available within the Supplementary Information.

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Author contributions

C.J.T. conceived the FTC concept, developed the computational demonstration and drafted the manuscript. T.D., C.R. and Y.L.D. contributed to the conceptual development and critically revised the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Christopher John Topping.

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